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PLANT SUCCESSION AND GRAZING CAPACITY ON CLAY SOILS IN SOUTHERN NEW MEXICO [1]

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INTRODUCTION

It is common knowledge that continued overgrazing, such as is prevalent on the semidesert ranges of the Southwest, reduces the stand of desirable forage plants and leads to serious range depletion, especially during periods of drought. Such depletion allows erosion of the valuable topsoil layer and permits rainfall to run off in torrential floods, with consequent damage to agricultural lands and urban property in the valleys. Native vegetation, therefore, plays an important rôle not only in range conservation and improvement but also in the protection of watersheds.

This report is concerned with the vegetation and especially with the plant succession found on various types of clay soils occupying nearly 32,000 acres, or approximately one-sixth, of the entire Jornada Experimental Range, and covering large areas in the southern portions of Arizona and New Mexico and the western part of Texas. Different areas of the soils studied present every stage of vegetative development from complete denudation to the climax of dense tobosa grass (*Hilaria mutica*). The denuded and seriously depleted areas present the most critical problems on range units, and their restoration is of the greatest importance. They are practically worthless for grazing and furnish no watershed protection. They also complicate management of the whole unit and are a factor in the silt accumulation of flood waters. They support *Drymaria holosteoides* and *Astragalus* spp., poisonous plants which cause serious losses of livestock. Sampson (*6*) [3] has shown that the grazing value of the vegetative cover is determined essentially by the stage of succession. Plant succession was studied on the range to determine how natural revegetation occurs and the grazing values produced by each stage of development.

SOURCES OF DATA AND METHODS OF INVESTIGATION

In connection with the natural-revegetation and range-management studies on the Jornada range since 1915, many valuable climatic and

[1] Received for publication June 18, 1931; issued January, 1932. In order to establish a complete range unit on which to conduct experiments and demonstrations in range management under conditions existing in southern New Mexico and similar areas in adjoining States, and to find a solution to the problems of range maintenance and grazing capacity which confront the stockmen of the region, the Jornada Experimental Range was created by Executive order May 3, 1912, upon recommendation of the Secretary of Agriculture. This range, upon which the investigations here detailed were carried out, contains approximately 193,000 acres. It is located in Dona Ana County, N. Mex., 10 miles east of the Rio Grande and about 50 miles north of the Mexican boundary. On August 1, 1930, it was made a branch station of the Southwestern Forest and Range Experiment Station.

[2] Acknowledgment is due the earlier members of the Jornada Experimental Range staff for collection of data prior to 1925. Valuable help was rendered by L. C. Hurtt, who established several quadrats for the purpose of studying successional changes of vegetation on clay soils. Constructive criticism of the report was given by Gordon D. Merrick and several other members of the Forest Service.

[3] Reference is made by number (italic) to Literature Cited, p. 1051.

vegetative records have been accumulated. Such of these as yielded significant data were incorporated in this report. Additional studies covering phases of the problem needing special investigation included a close study of soil and vegetative conditions in the field and detailed study of representative areas.

Maximum and minimum air temperatures have been observed daily, and precipitation has been measured at the range headquarters since July 1, 1914, in cooperation with the United States Weather Bureau. Records of evaporation from a free water surface and wind-movement data are taken from the United States Weather Bureau reports for Elephant Butte Dam (*4*). The station is reasonably comparable in evaporation and wind movement to the Jornada Experimental Range, as is shown by measurements taken at the range during 1929 and 1930.

The descriptions of soil types and characteristics were adapted from a report (1918) by J. O. Veach, of the then Bureau of Soils, United States Department of Agriculture, based upon his soil survey of the Jornada range.

The quadrat data were obtained from representative plots, 1 meter square, which were mapped from 1915 to 1924, inclusive, by the strap method, and from 1925 to 1929 by the chartograph method, as outlined by McGinnies (*5*). Perennial-grass tufts were mapped at a height of 1 inch above the ground and were compiled in square centimeters, or ten-thousandths of a square meter.

The degrees of grazing use presented in the analysis of factors influencing vegetative spread were recorded in June at the close of each grazing year as a part of the regular grazing-capacity project. These data record in percentages the volume of range feed used by grazing animals and are based upon the palatability and growth requirements of the forage plants.

Germination tests of the various grass seeds were made from 1923 to 1925 by the agricultural experiment station of the New Mexico College of Agriculture and Mechanic Arts; in 1926 by Carola V. Jackson (*1*) at the University of Chicago; and from 1927 to 1929 by the Bureau of Plant Industry, United States Department of Agriculture. The tests of Drymaria seed were made at the Jornada range in 1930.

Between 1923 and 1928, numerous attempts were made to introduce exotic plant species on the Jornada range. Seedlings of Chinese pistache (*Pistacia chinensis*), dwarf Asiatic elm (*Ulmus pumila*), tamarisk or French tamarix (*Tamarix gallica*), Russian mulberry (*Morus alba tatarica*), ailanthus (*Ailanthus altissima*), and Osage-orange (*Toxylon pomiferum*) were set out in the spring and watered during the dry period. Alfileria (*Erodium cicutarium*) was broadcast over a quarter of an acre and harrowed into the soil just before the beginning of the rainy season in 1926, and tests of wallaby grass (*Danthonia semiannularis*) were made in pots and in small planted areas in 1927.

Livingston porous cup atmometers were run at two stations, in the denuded clay soil type and in the Hilaria association, from June 1 to October 7, 1927, in order to compare the evaporating power of the air during the summer in the two habitats.

Line transects were made through a number of tension zones on all the soil types, to determine accurately the changes in vegetation caused by variation in soils, and the distribution of species over the soil types.

In order to determine the actual conditions prevailing on the different clay soil areas and to indicate grazing values of the stages of succession, a careful record was made of the plant composition on representative areas in the fall of 1929. By using these records and palatability percentages, determined for each species under different range type conditions by other observations and detailed studies, grazing-capacity estimates of the representative types were made. The same vegetative type may vary considerably between years of drought and of favorable climate, but the data were collected after four years of above-average precipitation and present the various stages in their best vegetative development between 1916 and 1930.

The estimates of grazing capacity are based upon the grazing reconnaissance method developed by the Forest Service.[4] In using this method upon a fairly uniform type of vegetation, the following ocular observations are necessary:

(1) The average reconnaissance plant density, or the proportion of ground covered by vegetation, expressed in tenths, and (2) the percentage each species contributes to the whole vegetative cover, with the various species grouped under the three following heads: Grasses and grasslike plants, "forbs" or weeds,[5] and shrubs.

These data, together with data on palatability, were used to obtain (1) the palatability factor of the type, or the proportion of vegetation of value as forage; and (2) the forage factor, or the factor for converting surface acres into forage acres.

Palatability is considered to be the degree to which the herbage within easy reach of livestock is grazed when a range is properly utilized under the best practicable range management. Thus, the percentage of the readily accessible herbage of a species that is grazed when the range is properly utilized determines the palatability of the species. Palatabilities, expressed as percentages, for the various species in this study have been developed from a close observation of proper forage use on the Jornada range since 1915.

The palatability percentage for each species is multiplied by the percentage of the stand represented by that species. The sum of the products for all species involved is the palatability factor of the type.

The forage factor is the product of the average reconnaissance density of the type times the palatability factor. A forage acre represents an acre completely covered with vegetation wholly valuable as forage. Grazing-capacity experiments on the range have shown that approximately 0.8 forage acre is required to support a cow and her calf, until it is weaned, for one month in the type of range under study. To determine the approximate number of surface acres of a type required to support a cow for a month, then, the figure 0.8 is divided by the forage factor. Table 1 is an example of the method used to obtain the grazing-capacity data. For the purposes of this report, each stage in the succession is considered individually with respect to grazing capacity, regardless of whether or not it actually occurs in uniform areas large enough to furnish the estimated number of surface acres required to carry a cow for one month.

[4] For detailed information on this method, see Instructions for Grazing Reconnaissance on the National Forests, 1927, which may be obtained from the Forest Service, U. S. Department of Agriculture, Washington, D. C.

[5] The term "forb" is applied to herbaceous plants other than grasses and grasslike plants.

TABLE 1.—*Sample illustration of vegetative composition, palatability, density, and grazing capacity of a Hilaria association* [a]

Species by classes of forage	Species composition	Species palatability	Species palatability factor [b]
Grasses:	*Per cent*	*Per cent*	
Hilaria mutica	75	60	0.450
Scleropogon brevifolius	20	20	.040
Forbs:			
Sphaeralcea spp.	1	60	.006
Perezia nana	2	0	0
Shrubs:			
Ephedra trifurca	1	10	.001
Flourensia cernua	1	0	0
Total	100		.497

[a] Reconnaissance plant density, 0.5. Forage factor (plant density × type palatability factor), 0.248. Approximate number of surface acres required to support 1 cow for a month on basis of 0.8 forage acre (0.8/0.248), 3.23.

[b] Species composition times species palatability.

FACTORS INFLUENCING VEGETATION ON CLAY SOILS

Since the vegetation on any area is controlled by habitat factors it is necessary to have a fairly complete picture of existing conditions and their causes. The factors influencing vegetative growth and change may be grouped under the following three main headings: Climatic, physiographic, and biotic.

CLIMATIC FACTORS

Because the culmination of favorable growth conditions occurs in the summer, climatic data for the Jornada range are more easily analyzed and correlated with vegetative response when considered by grazing years, or from July 1 to June 30 of the following calendar year. The principal measured climatic factors are thus summarized in Table 2, which shows the monthly means for temperature and precipitation at the Jornada range headquarters from July 1, 1914, to June 30, 1930, and for evaporation and wind movement at Elephant Butte Dam (*4*) from July 1, 1917, to June 30, 1930. On an average, these data show that although favorable growing temperatures may occur from March into October, yet on account of rainfall the growing season is limited mainly to three months, July to September, when slightly more than half of the total annual rainfall occurs. In some years the growing season may continue into early October, but low night temperatures usually render ineffective for the current season any rainfall after October 15. The culmination of unfavorable growth conditions is reached during the spring. Although temperatures become increasingly favorable during and following March, the precipitation is low, evaporation reaches its maximum in May and June, and wind movement is high during the entire spring period. Prevailing winds are from the west.

Evaporation varies considerably with the density of vegetation in different areas. As shown by Figure 1, evaporation from Livingston atmometers is consistently higher on a bare soil than in a Hilaria association. Thus the demands of the atmosphere upon seedlings in denuded soil are very severe, and only a limited number of species become established as pioneers.

TABLE 2.—*Means of principal measured climatic factors in experimental area*

Month	Temperature[a]		Precipitation[a]	Evaporation[b]	Wind movement[b]
	Daily maximum	Daily minimum			
	° F.	*° F.*	*Inches*	*Inches*	*Miles*
July	93.0	63.9	1.82	12.07	2,726
August	91.8	61.8	1.73	10.47	2,340
September	86.8	55.1	1.16	8.77	2,494
October	76.7	42.0	1.09	7.31	2,976
November	63.9	28.9	.42	3.93	2,453
December	53.1	22.2	.64	2.74	2,629
January	55.3	21.2	.28	2.78	2,638
February	62.5	26.4	.32	4.33	2,728
March	67.2	31.1	.48	7.46	3,544
April	74.0	39.1	.16	10.19	3,585
May	83.4	46.7	.64	12.86	3,583
June	94.7	56.2	.28	13.94	3,022
Average or total	75.2	41.2	9.02	96.81	2,893

[a] At Jornada Experimental Range headquarters, grazing years 1914–15 to 1929–30.
[b] At Elephant Butte Dam, grazing years 1917–18 to 1929–30.

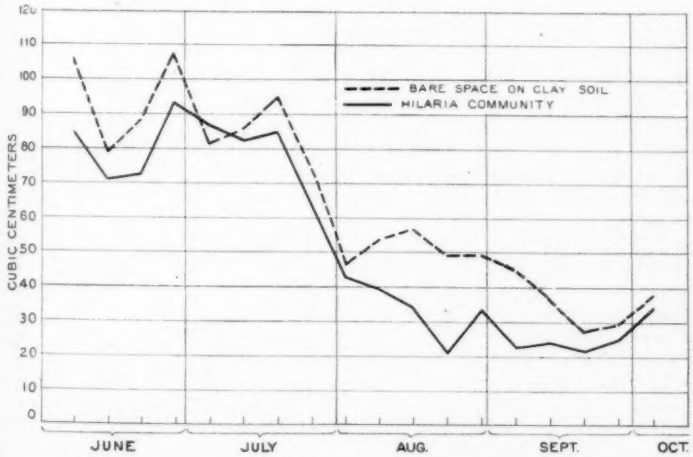

FIGURE 1.—Evaporation from Livingston atmometers, Jornada Experimental Range, 1927

PHYSIOGRAPHIC FACTORS

Since the vegetative composition of each stage of succession usually is different on different types of soil, it is necessary to consider the various clay soils found on the Jornada range. Within the limits of the range there are three topographic divisions, namely, the Jornada plain or mesa, the foothills, and the higher mountain slopes on the east.

The Jornada mesa is a gently undulating, featureless plain ranging between 4,000 and 4,600 feet above sea level. It is not occupied by any permanent stream and there is no surface outlet to the Rio Grande, which is 10 miles to the west. Arroyos extend from the foothills down the slopes of the plain for 1 to 5 miles. These are dry except after torrential showers, at which time the water debouching

from them spreads out over the sand or clay flats at their mouths and rapidly disappears by percolation and evaporation.

The geologic formations in the Jornada plain consist of unconsolidated deposits of alluvial wash derived from the adjacent mountain masses. The upper part of the deposits at least are Pleistocene in age and for the most part consist of interbedded, comparatively thin layers of reddish sand, buff, grayish, or chocolate-colored clay, and gravel or bowlders. A highly calcareous substratum or caliche, occurring at depths ranging from 15 inches to 4 feet, is characteristic. This layer consists of a concentration of calcium carbonate and, very probably, other salts. Its development is greatest under sandy or gravelly soils and slightest under tight clay soils.

The clay soils on the Jornada range can be grouped into three main classes, although each class has rather wide variations between different areas. These main types are clay or adobe soil, clay loam, and lake-bed clay.

The adobe soil occurs as extensive flats at the mouths of arroyos or in the lower, flatter parts of alluvial aprons. Toward the foothills these aprons ascend by broad, flat steps. The rise from one flat to the next is marked by an abrupt clay bank from 3 to 8 feet high. Each bank or terrace scarp probably marks the extreme point to which successive sheets of alluvium were carried by storm waters at different periods. Since the distance to which the alluvium spread decreased as the slopes were built up and the velocity of the water decreased, the material was deposited in a succession of overlapping sheets. In many places the wind has worked in front of the scarps, which, owing to the prevailing slope, face the west, sweeping out the sediment until the surface is quite bare and depositing sand on the edge of the higher terrace, thus increasing the height of the rise from one flat to another. The clays in this type are tight, compact, and impervious. When dry, the soil is extremely hard. Water from light rains sinks in only a few inches or stands in puddles. These characteristics make difficult the establishment and maintenance of vegetation on adobe soils. These soils are mainly a chocolate or dark red, but in places are grayish or buff.

The clay loam types are intermediate in texture and structure between the clay flats just described and sandy or gravelly soils. Soils of this class also occupy an intermediate topographic position on the slopes of the foothills. They are not uniform in texture but are rather a composite of a number of intimately associated lithologic phases, among which red, compact sandy clay loam predominates. In other places the material is a compact fine sandy loam, and in many areas considerable gravel is to be seen on the surface. Nearly all the clay loam soils are more pervious and have soil moisture conditions more favorable for plant growth than those of the adobe flats.

The lake-bed clay classification includes land occupying beds of both present intermittent lakes and of old or extinct lakes. In the extinct lakes the outlines are still well preserved, and desiccation was comparatively recent. The soil in these situations may be either a chocolate-red or a grayish fine-grained structureless clay, which is sticky and plastic when wet and extremely hard and impenetrable when dry. It is usually highly calcareous and may contain scattered crystals of gypsum. In places a thin veneer of fine sand has blown over the surface of the clay.

BIOTIC FACTORS

As Taylor (*7*) points out, the problem of grazing management is one of proper handling of the complex biotic communities occurring on ranges. These communities include not only the forage plants and livestock, but all the plants and native animals. Except for data on grazing intensities, biotic factors on the Jornada range are largely unmeasured. In fact, until 1930, no attempt was made to estimate the proportion of forage use by rodents as distinct from use by livestock. However, observations in 1929 and 1930 showed that the rodents on the range—mainly jack rabbits, cottontails, and kangaroo rats—live almost entirely on sandy soils, and so are of little direct consequence in this study except in the sand dunes found on the terrace crests in the adobe type.

PLANT SUCCESSION ON DIFFERENT TYPES OF CLAY SOILS

In order to present a complete series of successional stages, some areas absolutely without vegetation must be studied for the pioneer stages. Bare clay areas exist on the Jornada and adjacent ranges, and both economic and ecological considerations require some explanation of them, especially those which once supported vegetation but are now denuded.

Among causes of denudation, rainfall, which is often in the form of torrential cloud-bursts, is often of primary importance. Surface run-off is rapid after heavy rains, especially near the foothills and mountains. Where naturally sparse vegetation permits water to drain quickly from steep slopes, the more fertile topsoil is carried away, and gullies cut in rapidly, undermining vegetation and draining moisture from the adjoining soil. Among other causes of denudation are localized overgrazing, trampling or loitering of stock near bushes, and trailing of stock, especially in localities exposed to erosion by wind action or flood waters. As has been stated, most rodents prefer the more sandy soils for their burrows, but prairie-dog workings, which contribute to denudation, occasionally are found in the clay soil types. Another common factor in range destruction through the Southwest is the plowed land exposed to erosion on abandoned homesteads.

Artificial revegetation is usually the first method suggested for restoring plant cover on denuded soil, but, as is shown in Table 3, attempts to introduce exotic shrubs on the range have met with little success, and plantings of alfileria and wallaby grass, also exotics, failed to survive. However, Wilson (*8*) reports that fourwing saltbush or "chamiza" (*Atriplex canescens*), a shrub, and blue grama (*Bouteloua gracilis*) are promising native species for artificial reseeding in New Mexico.

TABLE 3.—*Survival of exotic shrubs on Jornada Experimental Range*

Species	Shrubs planted		Survival in 1929		Average height, 1929
	Year	*Number*	*Number*	*Per cent*	*Inches*
Chinese pistache [a]	1923	53	2	3.8	12
Dwarf Asiatic elm [a]	1923	175	[b] 5	2.9	61
Tamarisk	1923	20	0	0	------
Russian mulberry [a]	1927	2	0	0	------
Ailanthus [c]	1928	5	1	20.0	32
Osage-orange [c]	1928	5	1	20.0	19

[a] Seedlings obtained through courtesy of Bureau of Plant Industry.
[b] Exclusive of one tree 185 inches high, grown over a cesspool.
[c] Seedlings obtained through courtesy of the regional forester, Albuquerque, N. Mex.

It appears that the revegetation of denuded areas will be, at best, a long process and that it must be accomplished by native plants adapted to climatic and physiographic conditions of the region, which must be grazed to a degree conservative enough to permit their revegetation and maintenance. The restoration of a suitable plant cover on areas in various stages of depletion may be greatly facilitated by improved range and livestock management based upon a better understanding of successional processes and stages. The actual length of time required to restore areas in various stages of depletion will depend in part upon the seriousness of depletion of the most important plants in the succession, and upon soil conditions. Because of the different conditions affecting natural succession and the variations in plant cover in the successional stages on the different clay soil types, plant succession has been discussed separately in this paper on adobe soils, sandy clay loam, gravelly clay loam, and lake-bed clay. Table 4 shows the grazing capacity of these soils at various stages of succession and the variation of grazing values within each stage.

TABLE 4.—*Comparison of grazing capacity in various stages of succession on clay soils*

Stage	Soil type	Surface acres required per cow per month	
		For representative area	Range within each stage
		Acres	*Acres*
Lichen	Adobe, gravelly clay loam, lake-bed clay	50	15.1 and over
Localized ruderal-weed	do	25	15.1 to 35.
Ruderal-weed	Sandy clay loam	10.1	7.6 to 15.
Scleropogon	All soil types	5.8	5 to 7.5.
Mixed-grass	Sandy clay loam	5.4	4.5 to 7.5.
Flourensia-hilaria	Gravelly clay loam	3.4	3 to 7.5.
Hilaria	Adobe, lake-bed clay		

PLANT SUCCESSION ON ADOBE SOILS

The adobe soils occur in alluvial aprons, which ascend from the Jornada plain toward the foothills in broad, flat steps. Each step is marked by an abrupt clay bank or terrace scarp. In many places the wind has worked in front of the scarps, simultaneously sweeping the surface bare and depositing sand on the edge of the higher terrace. Many of these sand deposits are true moving dunes, which shift very slowly toward the east, driven by the prevailing west winds. The average annual wind movement for 13 years, as recorded at Elephant Butte Dam, is approximately 4 miles an hour. This, in itself, does not seem excessive, but bare spaces are scoured and sand on the terrace edges is moved by strong, unabating semihurricanes which occur intermittently during the spring and early summer.

The relief of the terrace edges, with their scattered dunes, makes it difficult for plants to invade these areas. In many places the difference in soil level between terraces may be 5 to 8 feet; this leads to unfavorable moisture conditions on both sides of the bank. Rain falling on the lee side drains quickly to the lower level, often forming small arroyos and contributing to the erosion of soil from the upper level. (Fig. 2.) The water drains so quickly from the higher level of soil that it is not available to the plants there and consequently

they are less vigorous than they would normally be. The water, after reaching the flat lower level, drains slowly and often stands in small puddles for several days before evaporating or sinking into the earth. Although drainage from above may promote seed dispersal of a few plants onto the lower clay flat, the standing water in the depression makes reseeding difficult.

Pioneer Lichen Stage

The first stage in the plant succession on adobe soils is the lichen stage. The uppermost 6 or more inches of bare clay soil are subject to greater fluctuations in moisture content than the corresponding layer in the same soil type in areas where there is a vegetative cover. The adobe softens quickly after rains, but the top layer, which is practically devoid of humus, hardens rapidly upon drying and con-

Figure 2.—Gullies on the outwash slope of an adobe terrace bank

tracts to form wide cracks. The soil is thus a poor habitat for most plants but an excellent base for the establishment and spread of a crustose lichen, *Lecidea crenata dealbata*, which is widespread in the region under study. This lichen scattered over the surface, although it has no forage value, protects the soil from wind erosion and builds up its humus content. (Fig. 3.)

Aside from lichens, scattered specimens of algae, *Nostoc commune flagelliforme*, and a few forbs, plants are scarce on bare adobe soils. The entire revegetation of such soils is characterized by the absence of a definite ruderal stage, except for a very limited number of species on the open flats and a fairly dense growth in drainage paths, where moisture is more abundant.

Localized Ruderal-Weed Stage

Although the bare adobe flats appear level, they have a slight degree of slope, and gravitational waters from heavy rains develop shallow drainage channels where seeds are easily disseminated and where moisture is more abundant than on the rest of the flat area. In such drainage paths a localized ruderal vegetation may develop, and some perennial grasses of considerable forage value may grow. The principal species found here are as follows, in order of their

abundance: *Hoffmanseggia jamesii*, globemallow (*Sphaeralcea incana*), *Hymenopappus robustus*, *Drymaria holosteoides*, *Amaranthus graecizans*, *Sporobolus airoides*, and *Scleropogon brevifolius*. In some areas, the Drymaria may cover the soil after heavy rains in August and September. This plant, however, offers a special problem which complicates the situation from an economic viewpoint.

Drymaria holosteoides Benth. (*D. pachyphylla* Woot. and Standl.), as Lantow (*3*) points out, "has proved itself to be one of the most deadly of the poisonous plants and losses of cattle in New Mexico have often, within a few months' time, run into thousands of dollars." It is a menace especially during the late summer and fall. It is a low, nearly prostrate annual of the Silenaceae. The plant occurs only on the hard soils, where no other vegetation is present, and in drainage paths where seed dispersal is facilitated and moisture con-

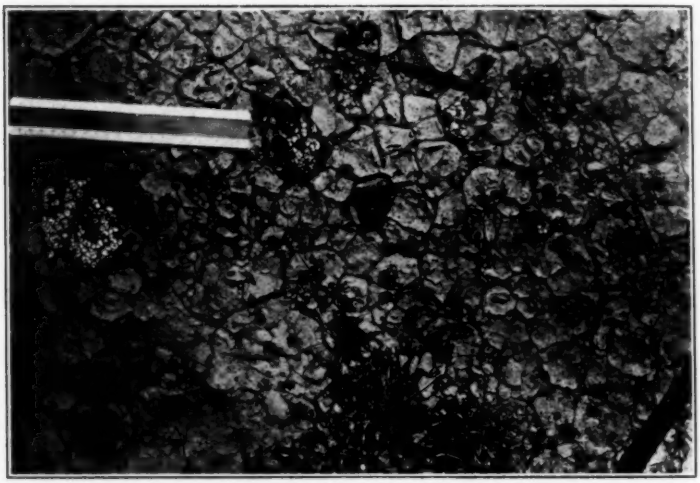

FIGURE 3.—Denuded adobe soil, with cracks in the surface crust. Nostoc is near the pencil point and Lecidea near the scale. Burro grass (*Scleropogon brevifolius*) is advancing onto the area

ditions are favorable. It grows very quickly and usually produces flowers and seeds within a few days after the seedling becomes established. Because of its abundant seed production it is extremely difficult to eradicate.

Drymaria holosteoides seed were collected in the fall of 1929 and germinated during the following winter. In a test made at room temperature during October, 1929, only 3 per cent germination was obtained. On January 12, 1930, two lots with 100 seeds in each were started, one at room temperature and one at about 40° F. On February 5, of those at room temperature 55 per cent had germinated. As none of the lot at 40° had started by January 22, these were allowed to dry out and (on February 2) 50 seeds were moved to room temperature and 50 left in the cold. No germination was observed in the latter lot, but on February 20 the lot at room temperature showed 66 per cent germination. On March 3, tests of seven additional lots

of 100 seeds each were started at room temperature. On March 27, these showed germination ranging from 25 to 50 per cent, with an average of 38 per cent.

These tests show that *Drymaria holosteoides* seeds are viable and have sufficient endurance to withstand alternate wetting and drying and finally to germinate when favorable conditions occur. The existence of this noxious species as a potential pioneer and the possibility of every bare clay surface becoming a poison area from its growth makes it not only desirable but necessary to hasten revegetation of other species.

Although areas supporting the localized ruderal stage are not of sufficient size to be considered grazing units, their grazing capacity should be calculated in a manner similar to that used for the better forage types. The localized ruderal weed stage affords only enough vegetation to support a cow for one month on approximately 50 acres. This low grazing capacity is better than none, but it is not compatible with the most economical livestock production. Furthermore, these practically denuded spots have no value for watershed protection and, even when small, endanger the watershed value of better, adjacent areas. This is an added reason for hastening revegetation of other species.

The Scleropogon or First Grass Stage

The first successional stage of any real forage value to become established on adobe soils is the Scleropogon. Fourteen years' study on the Jornada range has shown that *Scleropogon brevifolius* is the most suitable grass for the early natural revegetation of depleted adobe soils, although other pioneering grasses occur in the type. *S. brevifolius* spreads both vegetatively and by reseeding.

Scleropogon brevifolius, which has a root system extending 8 to 16 inches into the soil, is well adapted to efficient absorption from heavy clay soils where the moisture seeps downward very slowly from the surface. The mature plant because of its ability to conserve the available water supply by small size, restricted growth, and wide spacing of tufts can survive several years of below-average rainfall.

Scleropogon brevifolius may produce horizontal stolons from 6 to 10 inches long in a single year. These stolons have rooting sets at the nodes, as shown in Figure 4. The number of unrooted sets produced on two Scleropogon quadrats as indicating the possible rate of spread, is set forth in Table 5, together with seasonal and annual rainfall data. From 1915 to 1927, the grass was spreading over both quadrats, hence the greater number of sets in most years prior to 1929. No very close correlation between rainfall and the number of unrooted sets can be developed from this table, but it is significant that the greatest number of unrooted sets on both quadrats should have been produced in 1919–20, which had excellent summer-seasonal rainfall, and was immediately preceded by a year with above-average precipitation. Further, no sets were produced in 1916–17, which had the minimum summer-seasonal rainfall for the 16-year period, and set production was very poor in 1922–23, which had only 3.18 inches of rainfall during the summer. These data show that summer rainfall probably is most important in set production. Set production is much more prolific on the young pioneering *S. brevifolius* tufts than in the well-

established stand, as is shown by the fact that in 1929 quadrat L–3, with a tuft area of 2,631 sq. cm., produced only 7 sets, as compared with quadrat L–3a, which had a tuft area of only 176 sq. cm. and produced 15 sets. Quadrat L–3a adjoins L–3 and was established in 1929 in order to follow the vegetative spread of *S. brevifolius* after it had progressed beyond the limits of L–3.

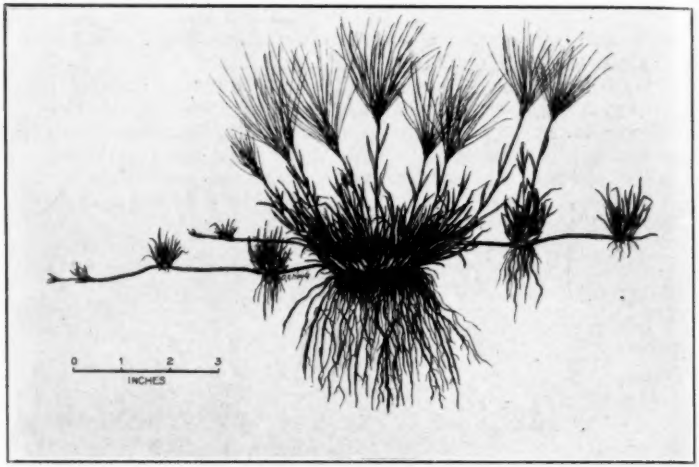

FIGURE 4.—Drawing of *Scleropogon brevifolius*, showing character of root system, foliage, stolons, and sets

TABLE 5.—*Rainfall and the production of unrooted sets by Scleropogon brevifolius*

Grazing year (July 1 to June 30)	Precipitation at Jornada headquarters		Unrooted Scleropogon sets [a]	
	Annual	Seasonal [b]	Quadrat L–3	Quadrat L–4
	Inches	*Inches*	*Number*	*Number*
1915–16	8.51	4.86		
1916–17	6.80	2.58	0	0
1917–18	3.62	2.34	(c)	(c)
1918–19	10.47	4.41	36	1
1919–20	14.05	8.20	92	43
1920–21	9.72	5.67	28	18
1921–22	4.80	3.49	50	14
1922–23	9.18	3.18	11	2
1923–24	7.45	3.95	36	14
1924–25	6.10	3.87	38	10
1925–26	10.48	3.76	29	3
1926–27	13.64	8.53	(c)	(c)
1927–28	9.09	6.33	(c)	(c)
1928–29	10.47	3.92	28	33
1929–30	9.11	6.18	7	10

[a] Quadrats charted in September or October near end of growing season.
[b] July, August, and September.
[c] Not charted.

The quadrat charts shown in Figure 5 demonstrate the possibility of revegetation of adobe flats and show the rate of spread of Scleropogon under the various conditions mentioned in Table 6. From a comparison of tuft area with precipitation, it is evident that the Scleropogon changes of tuft area vary rather closely with the precipitation

for the preceding year, unless the precipitation of the current or the preceding year is extreme enough to overbalance the vegetative changes which would ordinarily occur. It will also be noted that it was only after a period of several successive years, during which wind movement dropped to considerably below average, precipitation was favorable, evaporation below average, and grazing moderate to proper, that real progress was made in Scleropogon spread by stolons over

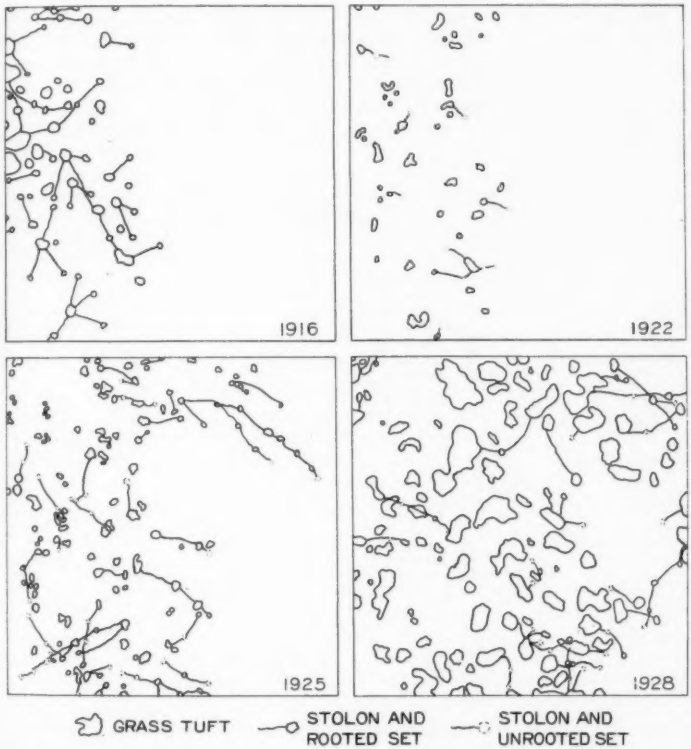

FIGURE 5.—Chartings of quadrat L–3, showing *Scleropogon brevifolius* tuft areas in 1916, 1922, 1925, and 1928

quadrats L–3 and L–4 and that substantial increases of tuft area were effected.

Definite conclusions concerning the effect of grazing on the Scleropogon spread can not be drawn from the data given in Table 6 because, during so much of the period under consideration, unfavorable climatic conditions caused poor forage production and consequently overgrazing prevailed in several years. The principal forage species in this stage of succession are palatable and nutritious to livestock only during the summer period. The Scleropogon tuft area responded favorably under moderate grazing, but the type as a whole was heavily grazed. Under light grazing from 1926 to 1929,

when climatic conditions were also favorable, Scleropogon made very substantial gains. The grazing intensities indicated in Table 6 apply to large areas made up of intermingled units of all stages of succession. As Hilaria is three times as palatable as Scleropogon, the Hilaria associations which grow more or less intermingled with this stage may be used heavily, and actual grazing on the less palatable Scleropogon of the same range may be lighter. As Jardine and Forsling (*2, p. 10*) state: "The burro grass [Scleropogon] begins growth early and has its main value as forage before other vegetation has greened; after that time it is grazed but little." The difference in palatability permits full use of the Hilaria types and results in a minimum interference with Scleropogon spread. Thus the establishment of Scleropogon may be accomplished under moderate grazing or even under full use of the range, especially where there are adjacent Hilaria areas.

TABLE 6.—*Precipitation,[a] wind movement, and evaporation,[b] and grazing use as related to Scleropogon tuft areas on quadrats L–3 and L–4, grazing years (July 1 to June 30) 1914–15 to 1929–30*

Year	Precipitation		Wind movement	Evaporation	Grazing use [c]	Tuft areas on—	
	Annual	Seasonal				Quadrat L–3	Quadrat L–4
	Inches	*Inches*	*Miles*	*Inches*	*Per cent*	*Sq. cm.*	*Sq. cm.*
1914–15	10.77	4.09					
1915–16	8.51	4.86			100		
1916–17	6.80	2.58			115	327	416
1917–18	3.62	2.34	35,025	110.38	115	[d]	[d]
1918–19	10.47	4.41	34,392	93.32	100	216	141
1919–20	14.05	8.20	35,588	95.99	90	279	174
1920–21	9.72	5.67	42,260	104.78	125	428	135
1921–22	4.80	3.49	36,134	105.16	130	430	159
1922–23	9.18	3.18	48,236	105.77	120	137	33
1923–24	7.45	3.95	44,980	92.63	100	303	71
1924–25	6.10	3.87	39,370	102.71	100	717	128
1925–26	10.48	3.76	30,582	87.43	5	262	51
1926–27	13.64	8.53	29,398	96.50	65	[d]	[d]
1927–28	9.09	6.33	27,134	89.44	50	[d]	[d]
1928–29	10.47	3.92	27,279	93.12	75	1,682	543
1929–30	9.11	6.18	20,956	81.30	100	2,631	1,116
Average	9.02	4.71	34,718	96.81			

[a] At headquarters Jornada Experimental Range.
[b] At Elephant Butte Dam.
[c] 100 per cent is proper for type as a whole.
[d] Not charted.

Observations of the Scleropogon on several quadrats charted from 1915 to 1929 and ocular observations of other areas show the establishment of some seedlings in favorable years. Germination percentages of *S. brevifolius* seeds collected from the Jornada range are as follows:

	Per cent		Per cent
1923	18.6	1927	60.0
1925	0	1928	30.0
1926	46.0	1929	78.5

Scleropogon seeds are produced in abundance during favorable seasons. By means of their long awns they are disseminated easily by the wind. The florets are needlelike and slightly twisted and cling tenaciously in cracks of the clay soil and to the scattered fila-

ments of Nostoc which adhere closely to the surface, even of dry soil. The germination tests demonstrate that the seeds are viable and field records show that seedlings become established. Because of its ability to reproduce both by means of stolons and of seed, Scleropogon is a very effective pioneer on denuded or depleted adobe soils.

One of the principal grass species associated with the Scleropogon is dwarf dropseed (*Sporobolus auriculatus*). The two species are so similar that they are often rather difficult to distinguish from one another unless their flower stalks are developed. They may be regarded as ecological equivalents, although the Sporobolus has underground rhizomes instead of aboveground stolons. These rhizomes grow horizontally just under the soil surface. They have numerous rooting nodes, and the new plants established from these nodes, unless they are exposed by soil erosion, are more stable than the aboveground sets of Scleropogon.

Sporobolus auriculatus produces small, hard seeds characteristic of the genus. Germination percentages of seeds collected on the range from 1925 to 1929 are as follows:

	Per cent		Per cent
1925	0. 3	1928	7. 0
1926	33. 3	1929	43. 5
1927	1. 5		

The seeds collected in 1926 were tested by Jackson (*1*), who, in retesting seeds saved from the 1925 sample, obtained 100 per cent germination as compared with the 0.3 per cent when the seeds were tested the same year they were collected. This shows that Sporobolus seeds may germinate poorly the first season, but that they have good viability and will germinate well eventually. Thus it is found that Sporobolus as well as Scleropogon is well fitted for establishment vegetatively and by seeding.

TABLE 7.—*Estimated vegetative composition, palatability, and grazing capacity of a representative Scleropogon type on adobe soil* [a]

Species, by classes of forage	Composition	Palatability	Palatability factor
	Per cent	*Per cent*	
Grasses:			
Scleropogon brevifolius	55	20	0. 110
Sporobolus auriculatus	23	20	. 046
Sporobolus asperifolius	8	20	. 016
Sporobolus airoides	6	50	. 030
Hilaria mutica	2	60	. 012
Forbs:			
Hoffmanseggia densiflora	2	50	. 010
Eschenbachia coulteri	1	0	0
Chamaesaracha coronopus	. 5	0	0
Solanum eleagnifolium	. 5	0	0
Shrubs:			
Flourensia cernua	1	0	0
Ephedra trifurca	. 5	20	. 001
Koeberlinia spinosa	. 5	0	0
Total	100		. 225

[a] Reconnaissance plant density, 0.35; forage factor, 0.079; approximate number of surface acres required to support a cow for 1 month, 10.13.

The Scleropogon type, as found on the Jornada Experimental Range, includes scattered specimens of other grasses, with a few forbs and shrubs, as shown in Table 7. This type, when used during the proper

season, requires approximately 10 surface acres to carry a cow for one month, as compared with approximately 50 acres required on the typical localized ruderal weed stage. Although the grazing capacity of the Scleropogon type is low, this stage represents a very tangible forage resource, especially in drought periods, and is infinitely superior to the scattered vegetation of the earlier stages of succession, both as range feed and as protection from erosion. In addition, this pioneer grass association plays a very definite rôle in building up the nutrient content and water-holding capacity of the soil, thus preparing it for the next stage of succession.

Hilaria Climax

The Hilaria or swale type, as it is commonly called, immediately succeeds the Scleropogon stage. *Hilaria mutica*, the dominant species of this climax stage, is a rather coarse sod-grass which spreads vegetatively by means of large rhizomes. (Fig. 6.) The root system is

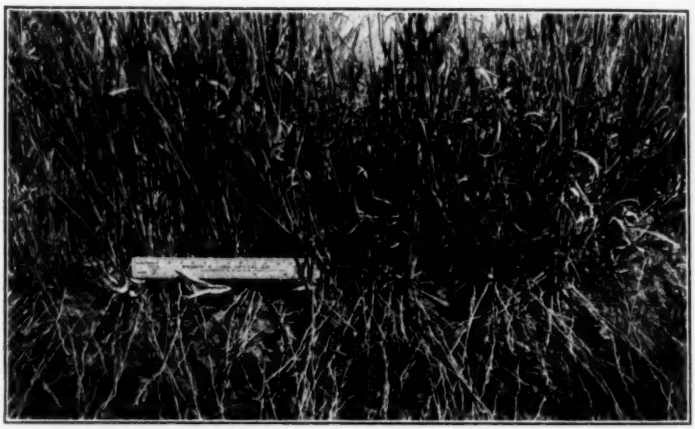

Figure 6.—Bisect of *Hilaria mutica*, showing the coarse root system and large rhizomes

coarse and poorly adapted to the most efficient absorption of moisture from the soil. The plants require flooding to make energetic growth, and for this reason the best developed stands of *H. mutica* always occur in depressions where surface run-off accumulates and stands for a few days. In fact, almost pure stands of *Hilaria mutica* form the semidesert climax on the adobe clay depressions.

The struggle between *Hilaria mutica* and *Scleropogon brevifolius* for dominance on adobe clay soils is shown rather strikingly by the results given in Table 8 for a quadrat, representative of an encroaching stand of tobosa grass. In 1915 the quantity of Hilaria on the plot was nearly three times that of the Scleropogon, although each largely occupied different parts of the quadrat. A material decrease in Hilaria tuft area occurred in 1919–20, as a belated result of the serious drought in 1917–18 and of overgrazing during the first five years of record. The Scleropogon responded more rapidly to the favorable growing conditions from the fall of 1918 to the spring of 1921, although the Hilaria had the greater density in the fall of 1921. Under overgrazing

and drought both species lost density rapidly between the fall of 1921 and that of 1922, and the tufts of each were greatly reduced in size. Although growing conditions were not especially favorable from the fall of 1922 to the fall of 1924, low densities on soil which had supported much higher densities and more moderate grazing than had prevailed earlier favored rather rapid recovery, especially of the good seeding and stolon-producing Scleropogon. The rather dry year of 1924–25 and low rainfall in the summer of 1925 caused a moderate setback in the development of both species. Then a steady recovery started again, Scleropogon being the more rapid in its development and reaching a maximum tuft area in the fall of 1927. By the fall of 1929 the Scleropogon had dropped considerably below its maximum, and Hilaria clearly dominated the quadrat, having reached its maximum tuft area for the entire 15-year period.

TABLE 8.—*Tuft areas of Hilaria and Scleropogon, precipitation, and grazing use on quadrat I–3, Jornada Experimental Range, 1914–15 to 1929–30*

Year	Precipitation		Grazing use [a]	Tuft area of—	
	Annual	Seasonal		Hilaria	Scleropogon
	Inches	*Inches*	*Per cent*	*Sq. cm.*	*Sq. cm.*
1914–15	10.77	4.09			
1915–16	8.51	4.86	130	595	209
1916–17	6.80	2.58	115	545	226
1917–18	3.62	2.34	220	(b)	(b)
1918–19	10.47	4.41	150	621	205
1919–20	14.05	8.20	145	273	284
1920–21	9.72	5.67	160	369	605
1921–22	4.80	3.49	125	602	424
1922–23	9.18	3.18	110	50	66
1923–24	7.45	3.95	105	108	236
1924–25	6.10	3.87	100	330	685
1925–26	10.48	3.76	5	287	473
1926–27	13.64	8.53	15	482	1,043
1927–28	9.09	6.33	100	662	1,327
1928–29	10.47	3.92	20	821	1,203
1929–30	9.11	6.18	100	1,278	779
Average	9.02	4.71			

[a] 100 per cent is proper for type as a whole. [b] Not charted.

The Hilaria reacted more slowly to climatic conditions than did the Scleropogon, but after periods of favorable rainfall Hilaria predominated, as is shown by the tuft areas of the two species in the autumns of 1915, 1921, and 1929. The lack of flood water in drought years arrested the succession, and the Hilaria recuperated more slowly than the Scleropogon. In the charting in the fall of 1918 it was difficult to distinguish the dead tuft areas of both species because of the small amount of green material produced in that dry summer. This fact accounts in part for the sharp reduction in tuft areas recorded in 1919, when the live tufts were easily recognized by their green foliage. It must also be remembered in interpreting Table 8 that the Scleropogon on the plot was lightly grazed in most years, owing to the higher palatability of the Hilaria. The estimates of forage use were made in June at the close of each grazing year. Even the Hilaria was not seriously overgrazed except from 1917–18 to 1920–21, since its palatability of 60 per cent is based partly on the proper use of plants even more palatable than it is. Just as occurred in recent

years on the quadrat recorded in Table 8, it has been observed on other areas that where a dense stand of *Hilaria mutica* encroaches upon a Scleropogon community the Scleropogon is the first species to give way. *Sporobolus auriculatus* gives way next, and *S. asperifolius* persists the longest, apparently because of its shade tolerance and a greater ability to withstand root competition.

The vegetative spread of *Hilaria mutica* is necessarily slow, but, as is true for most of the species of the region, vegetative reproduction is by far the surest method of migration. Very few seedlings of Hilaria have been charted on the Jornada range quadrats or recorded in the field notes, notwithstanding the generally high germination percentages (Table 9) obtained in the laboratory with seeds collected from the range.

TABLE 9.—*Germination percentage of seeds of Hilaria mutica collected from the Jornada experimental range*

Year	Germination in—		Year	Germination in—	
	Lot 1	Lot 2		Lot 1	Lot 2
	Per cent	*Per cent*		*Per cent*	*Per cent*
1923	66.3		1927	21.5	39.0
1924	5.0		1928	6.5	29.0
1925	66.0		1929	0	87.0
1926	34.0	91.0			

The variability in germination of seed in different samples is shown well by results when two lots were tested in the same year. The germination of the 1926 seeds indicated that higher germination percentage might be closely correlated with higher rainfall, as shown in Table 10. The seasonal precipitation was 4.82 inches in the region where lot 1 was collected and 7.51 inches in the lot 2 region. In preliminary tests, with seeds from the same samples, increased germination was generally obtained with successive trials.

TABLE 10.—*Percentage of germination obtained with Hilaria mutica seeds in successive trials, 1927*

Date	Germination in—		Date	Germination in—	
	Lot 1	Lot 2		Lot 1	Lot 2
	Per cent	*Per cent*		*Per cent*	*Per cent*
Jan. 19–Feb. 18	10	60	Feb. 12–Mar. 15	20	80
Feb. 4–25	20	100	Feb. 21–Mar. 16	34	91

From the germination results, it appears that seedling spread should be more important in the Hilaria invasion than it actually is. The fluctuating climatic conditions of late spring and early summer are undoubtedly responsible for lack of seedlings. Rains in May or June are often sufficient to cause germination, but both months regularly have long dry, windy periods during which it is almost impossible for seedlings to survive.

Because of its propagation by rhizomes, *Hilaria mutica* may be grazed during the summer season up to 60 per cent of its forage

production without injury. In fact, studies by Canfield [6] on the Jornada range showed that frequent clipping of this species at 2 inches from the soil surface stimulated increased tuft area for the first two years of the experiment. However, the stimulation was not permanent and the increase in dry weight of forage produced was not proportionately as great as the increase in tuft area. On the other hand, frequent clipping at 4 inches or even a single clipping at the end of the growing season each year at 2 inches produced a steady increase in tuft area during the first five years of the experiment.

The vegetative composition of a representative Hilaria type is set forth in Table 11. This type when grazed properly during the summer and early fall will support a cow for one month on approximatey 3.4 surface acres. Here again the desirability of managing the range to bring about the higher stage of succession is very evident when the grazing capacity of this climax stage is compared with that of the Scleropogon stage, wherein 10.1 surface acres are required to carry a cow for one month.

TABLE 11.—*Estimated vegetative composition, palatability, and grazing capacity of a representative Hilaria mutica association on adobe soil* [a]

Species, by classes of forage	Composition	Palatability	Palatability factor
Grasses:	*Per cent*	*Per cent*	
Hilaria mutica	66	60	0.396
Scleropogon brevifolius	10	20	.020
Sporobolus airoides	6	50	.030
Sporobolus auriculatus	5	20	.010
Sporobolus asperifolius	4	20	.008
Bouteloua barbata	1	10	.001
Forbs:			
Gutierrezia sphaerocephala	2	0	0
Chamaesyce albomarginata	1	0	0
Perezia nana	1	0	0
Sphaeralcea incana	1	50	.005
Hoffmanseggia densiflora	.5	50	.002
Wedeliella incarnata	.5	20	.001
Shrubs:			
Flourensia cernua	1	0	0
Ephedra trifurca	.5	20	.001
Koeberlinia spinosa	.5	0	0
Total	100		.474

[a] Reconnaissance plant density, 0.5; forage factor, 0.237; approximate number of surface acres required to support a cow for 1 month, 3.38.

Although *Hilaria mutica* dominates this stage the principal grass species of the Scleropogon stage persist. *Sporobolus airoides* is one of the main associated species. Its seeds remain viable for several years, because of the hard, waxy seed coats. Seeds collected in 1925 and tested that year showed only 77 per cent germination, whereas 100 per cent germination was obtained from the same sample a year later. The plant migrates more quickly than *H. mutica*, especially in shallow drainage paths where seeds are dispersed easily and more moisture is available.

Experience on the Jornada range has shown that the Hilaria type must be used during the growing season if it is to be utilized when at its maximum grazing capacity. The grass is palatable to livestock only when it is green and succulent. It may be grazed to some

[6] CANFIELD, R. H. THE EFFECTS OF INTENSITY AND FREQUENCY OF CLIPPING BLACK GRAMA AND TOBOSA GRASS ON YIELD. 1930. (Thesis, Yale School of Forestry.)

advantage in the fall, but after growth has ceased the stems and leaves become so dry and tough that they retain little value and are refused by stock if other feed is available. An additional reason for using the Hilaria type during the summer is the opportunity thus afforded to defer grazing on the adjacent *Bouteloua eriopoda* range, so that the grass species growing in that type, which are palatable during the winter, may be allowed to produce the maximum volume of forage before being grazed.

Near the adobe terrace edges, where shifting sands encroach upon *Hilaria mutica* associations to the east, Hilaria is the first species to give way. It is replaced by a sparse stand of alkali sacaton (*Sporobolus airoides*). When the dune is quite large, the Sporobolus is killed by the advancing sands, and even the brush species die. Brush, however, often survives the sand deposition and perishes only after the soil is eroded from its roots. Such erosion occurs on the windward side of the terrace. *Flourensia cernua* may survive even a slow root exposure, as it is a very adaptable shrub which spreads by sprouts.

PLANT SUCCESSION ON CLAY LOAM SOILS

The clay loam types are intermediate in structure and geographic position between the adobe flats and adjacent sandy or gravelly soils. Through long periods of time the sandy or gravelly materials have gradually mixed with the clay where the soils overlap. The plant succession on the sandy clay loam is so distinct from that on the gravelly clay loam as to require a separate presentation.

Sandy Clay Loam

On sandy clay loam soils the lichen stage fails to develop. The ruderal-weed stage on this type of soil has both a more dense and a more diverse composition than the localized ruderal-weed stage on adobe soils. The more palatable forbs are *Hoffmanseggia densiflora*, *Sphaeralcea incana*, and *Lesquerella fendleri*, none of which occur commonly on the adobe soils. Scattered specimens of Scleropogon, *Muhlenbergia arenicola*, and *Sporobolus* spp. add to the forage value of the stage. The stage also includes some forbs worthless as forage, such as *Gutierrezia sphaerocephala*, *Croton corymbulosus*, and *Perezia nana*. This stage requires approximately 25 acres to support a cow for one month. The Scleropogon stage develops very much as on the adobe soils. Finally other grass species, growing more abundantly on near-by areas, become established to form a mixed-grass association, with a vegetative composition like that shown in Table 12. This is essentially a Scleropogon-Hilaria-Sporobolus association, but the main forage species is *Hilaria mutica*, although it is not dominant. This mixed-grass type must be grazed conservatively enough to encourage the growth of Hilaria, Aristida, Muhlenbergia, *Sporobolus airoides*, and *S. cryptandrus*.

All these species are palatable mainly during the summer and fall, and when feed is urgently needed grazing can hardly be deferred until winter to protect the scattered stand of highly palatable *Bouteloua eriopoda*. Where the soil contains a large percentage of sand and additional sand is deposited by the wind, the area eventually may develop into a Bouteloua association, but this succession is too long a process to accomplish within a single generation. For prac-

tical purposes, then, the mixed-grass type with its grazing capacity of 5.8 acres per cow per month, must be considered as the sandy clay loam climax. It should be stocked conservatively enough to maintain the more palatable species.

TABLE 12.—*Estimated vegetative composition, palatability, and grazing capacity of a representative mixed-grass type on sandy clay loam soils* [a]

Species, by classes of forage	Composition	Palatability	Palatability factor
	Per cent	*Per cent*	
Grasses:			
Scleropogon brevifolius	26	20	0.052
Hilaria mutica	17	60	.102
Sporobolus auriculatus	12	20	.024
Sporobolus asperifolius	7	20	.014
Sporobolus airoides	7	50	.035
Muhlenbergia arenicola	6	50	.030
Bouteloua eriopoda	5	80	.040
Aristida pansa	3	60	.018
Sporobolus cryptandrus	2	60	.012
Bouteloua barbata	1	10	.001
Forbs:			
Hoffmanseggia densiflora	1	50	.005
Sphaeralcea incana	1	50	.005
Lesquerella fendleri	1	20	.002
Chamaesaracha coronopus	1	0	0
Bahia dealbata	1	0	0
Aster leucelene	.5	0	0
Croton corymbulosus	.5	0	0
Perezia nana	.5	0	0
Aplopappus australis	.5	0	0
Shrubs:			
Gutierrezia sarothrae	3	0	0
Ephedra trifurca	2	20	.004
Prosopis glandulosa	1	10	.001
Yucca elata	1	10	.001
Total	100		.346

[a] Reconnaissance plant density, 0.4; forage factor, 0.138; approximate number of surface acres required to support a cow for 1 month, 5.80.

GRAVELLY CLAY LOAM

This soil phase contains only a small percentage of gravel, which is usually in a very scattered layer near the surface. The plant succession on gravelly clay loam is similar both in amount and composition of the plant cover in each of the early stages to that on adobe clays, the lichen, localized ruderal weed, and Scleropogon stages all occurring in the order named. The next step is the establishment of an open stand of brush, principally *Flourensia cernua*. This plant is a shrubby composite which seeds readily. When mature it is 3 to 4 feet high. Its growth rate is slow, but it spreads by vegetative means so that its advance over the Scleropogon stage (fig. 7) is very steady, once it becomes established.

The spacing of the Flourensia bushes is such that the Scleropogon plants are not immediately crowded out. The earliest phase is really a Flourensia-Scleropogon community, but the shrub, although not a forage plant, affords protection from grazing and improves soil conditions for the establishment of grasses which are palatable to livestock. These species, whose seeds are disseminated by wind and flood waters, are principally *Hilaria mutica*, *Muhlenbergia porteri* (a very edible grass that grows mainly in the shade of the shrubs), *Sporobolus airoides*, and *Bouteloua curtipendula*. With these new species established, the climax Flourensia-Hilaria association presents a vegetative composition as shown in Table 13. It will support a cow for one month on approximately 5.4 surface acres.

TABLE 13.—*Estimated vegetative composition, palatability, and grazing capacity of a representative Flourensia-Hilaria association on gravelly clay loam* [a]

Species, by classes of forage	Composition	Palatability	Palatability factor
Grasses:	*Per cent*	*Per cent*	
Hilaria mutica	26	60	0.156
Scleropogon brevifolius	11	20	.022
Muhlenbergia porteri	10	85	.085
Sporobolus auriculatus	10	20	.020
Sporobolus airoides	8	50	.040
Sporobolus asperifolius	5	20	.010
Bouteloua curtipendula	3	60	.018
Andropogon saccharoides	2	50	.010
Forbs:			
Perezia nana	2	0	0
Eschenbachia coulteri	1	0	0
Hoffmanseggia densiflora	1	50	.005
Chamaesyce albomarginata	.5	0	0
Eriogonum abertianum	.5	0	0
Shrubs:			
Flourensia cernua	17	0	0
Gutierrezia sarothrae	1	0	0
Lycium pallidum	1	0	0
Ephedra trifurca	.5	20	.001
Koeberlinia spinosa	.5	0	0
Total	100		.367

[a] Reconnaissance plant density, 0.4; forage factor, 0.147; approximate number of surface acres required to support a cow for 1 month, 5.44.

FIGURE 7.—The stages of succession on gravelly clay loams: Scleropogon advancing over a lichen stage in the foreground, with Flourensia shrubs encroaching from the background

PLANT SUCCESSION ON LAKE-BED CLAY

Lake-bed clay includes soils in lake beds, both present intermittent lakes and old or extinct lakes. In the extinct lakes the succession is identical with that on adobe soils, except where a thin layer of sand has blown over the surface. In this case, the lichen stage fails to develop, and the ruderal-weed stage is more clearly defined, with a good stand of *Hoffmanseggia densiflora*, *Evolvulus pilosus*, and *Actinea odorata*. Scleropogon and Hilaria stages then occur in regular order. *Hilaria mutica* develops in dense, almost pure stands where flood waters accumulate and remain for a few days but *Scleropogon brevi-*

folius remains dominant where moisture is less abundant. Where water stands for more than a few days, the area becomes an intermittent lake and is characterized by somewhat different vegetation.

On the Jornada range there are four intermittent lakes, which are completely dry during years with below-average rainfall but which hold water for three months to a year when rainfall is average or above. With the habitat varying between submerged and dry sun-baked conditions, it is almost impossible for a stable association to become established. For a period of several years the extreme edge of the water may remain low enough to permit the Hilaria climax to start, but one year with exceptionally high rainfall may see this association submerged for a prolonged period and killed. When the water level reaches an unusual height and remains there for several months, *Hilaria mutica* is the first plant to die; *Sporobolus airoides* persists longer but finally is killed. *Panicum obtusum* and *Distichlis spicata* thrive when submerged a few inches but grow very slowly after the water recedes. After the water percolates into the soil or evaporates, the ruderal-weed stage develops quickly where other vegetation has been killed.

SUMMARY AND CONCLUSIONS

In the semiarid Southwest it is extremely important to manage range units so as to maintain the best possible stand of vegetation, both for watershed protection and for sustained livestock production.

Drought, overgrazing, erosion by wind and water, and activity of rodents are all factors in range depletion. Grazing is the factor most easily regulated where the range is under some form of control.

Where depletion has become serious, the artificial reseeding of native forage plants during favorable climatic years offers some promise of success, but the introduction of known exotic species holds little promise. The satisfactory artificial reseeding of large areas of semidesert range in the Southwest would be a costly process. It is far better to maintain a good stand of forage through conservative grazing than to be forced to attempt artificial reseeding of the range after it has been depleted by overgrazing.

Seriously depleted clay soils may be restored by the natural succession of plants from pioneer stages, when the plants have little or no forage value, to climax stages in which only from 3.4 to 5.8 acres are required to support a cow for one month. A valuable cover does not become established immediately because the succession may require many years or even decades to complete.

The occurrence and plant composition of each stage in the succession is determined largely by the type of soil and its associated habitat factors. Each stage builds up the humus content and water-holding capacity of the soil, thus preparing it for the next stage until the climax is reached.

Drymaria holosteoides, a quickly developing annual herb which is poisonous to livestock, may occur in the pioneer ruderal-weed stages on adobe clay, gravelly clay loam, and lake-bed clay. It grows most abundantly on hard clay soils where no other vegetation occurs.

On all types of clay soils, the *Scleropogon brevifolius* association is the first grass type of any real or permanent forage value to become established. Scleropogon can survive several years of below-average rainfall.

Scleropogon spreads to new areas mainly by means of horizontal stolons which extend out over the soil surface from the parent plant and take root at the nodes. Summer rainfall is the most important single factor influencing the growth of stolons, although they are produced more abundantly by young Scleropogon plants than by plants several years old. The increase or decrease in size of the Scleropogon tufts is determined mainly by the rainfall of the preceding grazing year, unless the current summer-seasonal rainfall is sufficiently extreme to overbalance the changes that should have occurred.

Hilaria mutica, a sod grass, is either predominant or makes up a large proportion of the climax stage on all clay soil types.

When the climax Hilaria association encroaches upon the Scleropogon stage, the competition is very keen. Drought and overgrazing rapidly reduce the tuft areas of both the Hilaria and the Scleropogon, but during favorable climatic periods Scleropogon recovers rapidly. Hilaria recovers more slowly but eventually predominates in the competition.

The main spread of *Hilaria mutica* is by its rhizomes. It may be grazed up to 60 per cent of its herbage production each summer without injury or without materially hindering the succession on adjacent areas supporting lower stages. Hilaria should be grazed in the summer, because after maturity its foliage becomes so coarse that its palatability is practically nil.

Control and regulation of the range which would restrict livestock to the clay soil types during the summer, when their grazing value is greatest, would permit the plants in large *Bouteloua eriopoda* types on adjacent sandy or gravelly soils to mature unhindered. Thus the Bouteloua types could be reserved for use during the late fall, winter, and early spring, when they can be used to best advantage and when the clay soil types support little or no forage.

The main types of clay soils on the Jornada Experimental Range and adjacent ranges of the Southwest are adobe clay, clay loam, and lake-bed clay. The abode flats were formed by the deposition of alluvium at the mouths of arroyos; they occur as broad aprons with terrace scarps at the edges. In front of the scarps the wind sweeps out the soil and piles it on top of the terrace edges, thus further increasing their height.

There are four main stages of succession on adobe soils. The earliest pioneers are algae and lichens, which help to protect the soil surface from erosion and build up its humus content. The second pioneer stage is a localized ruderal-weed association which is confined mainly to shallow drainage paths but which often contains fairly dense stands of *Drymaria holosteoides*, a forb poisonous to livestock. The first stage of value as forage is the Scleropogon association, in which there is a good stand of grasses, with *Scleropogon brevifolius* predominant. The climax stage consists of *Hilaria mutica* with its associated species and furnishes more forage per unit of area than any of the preceding stages.

Clay loam soils are intermediate in texture and location between the adobe flats and either sandy or gravelly soils. The succession on gravelly clay loams is very similar to that on adobe clays, except that *Flourensia cernua*, a shrubby composite, is prominent in the climax. On sandy clay loams, the lichen stage is lacking, the ruderal-weed

stage is better developed, the Scleropogon stage is not clearly defined, and the climax is more a mixed-grass association, with *Hilaria mutica*, *Scleropogon brevifolius*, and *Sporobolus* spp. predominating.

The succession in extinct lake beds is similar to that on adobe soils, with an almost pure stand of *Hilaria mutica* as the climax. In intermittent lake beds, the alternate flooding and drying are so detrimental to orderly succession that no definite sequence of stages occurs. The Hilaria climax may occur to some extent beyond the high-water mark, and *Sporobolus airoides* grows even farther into the lake bed. Both species, however, are killed by too long a period of submersion. When dry the lake beds support a good stand of ruderal weeds.

Range management is complicated by the necessity of using all the successional stages during the summer growing season and early fall if their maximum grazing capacity is to be obtained and if large adjacent Bouteloua types suitable for winter grazing are to be reserved for their proper season of use. This immediately brings up the question of how to manage the range in order to bring about the succession and maintain the climax after it has developed.

The problem becomes one mainly of accurately determining the actual grazing capacity of each range unit, together with the best season for use and extent of variation due to drought, and finally of stocking the range during a suitable season on a basis conservative enough and with sufficiently uniform distribution of stock to bring about the desired vegetative trend, keeping an accurate check on vegetative conditions through reliable quantitative measurements.

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CONTROL OF GASTROINTESTINAL PARASITES OF SHEEP BY WEEKLY TREATMENTS WITH VARIOUS ANTHELMINTICS [1]

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PURPOSE OF EXPERIMENT

In controlling stomach worms and some other worm parasites of sheep in the North, the Middle West, and States as far south as Virginia, medicinal treatment with suitable drugs once every three to four weeks proved to be adequate. When the same problem of control was attacked in the South with its different climate and its sheep heavily stocked on dense pastures, this procedure was found to be ineffective, and it was necessary to treat every two weeks to control the parasites. Even then certain parasites, notably the small trichostrongyles, were not adequately controlled (*10*).[2]

The present experiment was undertaken to determine whether eradication of the worms previously controlled or the control of more kinds of parasites, especially small trichostrongyles, in sheep with very restricted range could be attained with safety by more frequent treatments. To this end, sheep were treated once each week for a year. The anthelmintics used in the experiment were copper sulphate in a 1 per cent solution, carbon tetrachloride, and tetrachlorethylene.

PREVIOUS INVESTIGATIONS

The copper sulphate treatment for the common sheep stomach worm, *Haemonchus contortus*, was developed by Hutcheon (*5, 6, 7, 8*) in South Africa. The treatment was tested critically by Hall and Foster (*2*) and found to be effective for the removal of *H. contortus* but of little or no value for other nematode parasites in the stomach and intestinal tract.

Hall and Shillinger (*3, 4*) tested carbon tetrachloride on sheep. They found that it was effective against *Haemonchus contortus* and the sheep hookworm, *Bunostomum trigonocephalum*, and partly effective against species of Nematodirus, Cooperia, Trichuris, and Oesophagostomum.

Hall (*10, Rpt. 1925–26*), as referred to by Mohler, reported that the results obtained from the treatment of a flock of sheep with tetrachlorethylene at various intervals for a year did not indicate that the drug was any improvement over carbon tetrachloride for use with sheep.

EXPERIMENTAL PROCEDURE

Eight mature sheep were used at the beginning of the experiment, which was conducted at the experiment station of the bureau at Bethesda, Md. Four of the 8 sheep were ewes that had been bred

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[2] Reference is made by number (italic) to Literature Cited, p. 1069.

before they were selected for the experiment, 2 were nonpregnant ewes, and 2 were rams. The 4 pregnant ewes were treated as follows: One received a 1 per cent solution of copper sulphate, 2 received carbon tetrachloride, and 1 received tetrachlorethylene. The division was made in this manner so that each of the 3 lots that received treatment would contain 1 or more pregnant ewes. Thus it would be possible to determine whether the respective anthelmintics had any effect on pregnant ewes, and to follow the subsequent degree of worm infestation in the lambs born to ewes in the different lots. One nonpregnant ewe received a 1 per cent solution of copper sulphate and one ram received tetrachlorethylene. The other ram and nonpregnant ewe made up the control lot.

The 8 sheep were thus divided into 4 lots of 2 sheep each, the lots being placed in adjoining pens, each 7 by 24 feet in size, separated from one another by a wire fence. Small pens were used in order that the sheep might be exposed to continuous heavy infestations of parasite larvae, a procedure which would not have been possible had the animals been permitted to roam over a large area. Under the conditions of the experiment, any control obtained could be credited to the anthelmintic and not to a combination of anthelmintic medication and light stocking. The conditions thus presented a severe test of the value of anthelmintic medication.

At the beginning of the experiment the pens contained sparse vegetation but this was soon eaten off by the sheep and in two to three weeks the pens were bare, and remained so during the rest of the experiment. Drainage was so arranged that none of the pens drained into others at any time during the experiment. A small floored shelter was provided at one end of each pen. Each lot of sheep was kept constantly on the same area during the experiment. As this ground had never before been used for sheep, the animals were not subjected to infection from parasite material already present.

The experiment began on October 22, 1928, and ended on November 25, 1929. One animal (754) which received copper sulphate solution died on November 21, 1928, and sheep 638 was substituted for it. Two sheep (761 and 738) which received carbon tetrachloride died, respectively, on June 15 and June 22, 1929. Sheep 753, which received copper sulphate solution, died on September 5, 1929. The other animals remained in the experiment until it terminated.

At the beginning of the experiment all sheep were fed a ration consisting of oats and mixed clover and timothy hay. The grain was fed from boxes, but the hay was placed on the ground. The sheep spilled a considerable part of the grain at different times, but no effort was made to prevent them from eating the grain from the ground as it was desirable that they should be exposed as much as possible to infective larvae of the parasites. The two animals that received carbon tetrachloride showed symptoms of calcium tetany after the first treatment and alfalfa meal was immediately added to their ration and to the ration of the two animals that received tetrachlorethylene, in an effort to build up the calcium reserve of the animals. The grain ration for these two lots then consisted of equal parts of oats and alfalfa meal. The sheep treated with carbon tetrachloride continued to receive this ration up to the time of death, but on February 25, 1929, the alfalfa meal was withdrawn from the ration of the sheep treated with tetrachlorethylene. As calcium tetany is not

known to be associated with the administration of the 1 per cent copper sulphate solution, the sheep receiving this anthelmintic, as well as the control sheep, were fed only the oats-and-hay ration. Sodium chloride in the form of rock salt was kept before the animals in each pen at all times.

The animals were treated once a week, except at the times noted in Figure 1. Each animal in the first lot received once a week 100 c. c. of a 1 per cent solution of copper sulphate by drench. Each animal in the second lot received once a week 5 c. c. of carbon tetrachloride in a No. 11 hard gelatin capsule filled with dry magnesium sulphate. Each animal in the third lot received once a week 5 c. c. of tetrachlorethylene in a No. 11 hard gelatin capsule filled with dry magnesium sulphate. The fourth lot served as a control and was not dosed. All treatments were administered before the morning feeding.

To determine the approximate degree of infestation, the writers made weekly parasite-egg counts from feces collected from each animal on the morning of treatment before the animal was dosed. For this purpose the animals were confined in separate compartments of the shelters. The floors were carefully swept just before the collection of feces, and an effort was made to collect samples from the top layer of the feces in order to have material that had not touched the floor. At times the samples may have been contaminated by parasite eggs previously deposited on the floor, but during the course of the experiment, extending somewhat over a year, it is very improbable that any such accidental contamination would appreciably affect the results. As a further check against such contamination, embryonated eggs and eggs in an advanced stage of segmentation were not recorded in the counts.

The egg-counting technic, a modification of the method of Stoll (*14*) and of Stoll and Hausheer (*15*), was as follows: Ten grams of feces was weighed and placed in a 500 c. c. Erlenmeyer flask, etched at the 300 c. c. mark. A quantity of 0.1 N sodium hydroxide solution sufficient to cover the feces was added to the flask, which was allowed to stand overnight in the refrigerator. The following morning a sufficient quantity of 0.1 N sodium hydroxide solution was added to bring the mixture up to the 300 c. c. mark, and the contents were shaken with glass beads until the feces were thoroughly comminuted. A 0.075 c. c. drop of the fecal mixture was then transferred to a slide. Two or more counts were made from each sample, each egg found upon the slide at this dilution indicating 400 eggs per gram of feces. The data given in Figure 1 represent the greatest number of eggs per slide, and not the average. No effort was made to determine the moisture content of the fecal samples, for an average tending to balance slight variations was, no doubt, attained over a year's time. The eggs of various strongyles were not classified, since the egg counts are intended merely to indicate, as far as such a count is indicative, the relative degree of infestation with nematode parasites and the actual variation after treatment.

RESULTS OF EXPERIMENT

In presenting the results of the experiment there are given (1) the egg counts on each individual sheep (fig. 1), these counts indicating the relative degree of infestation at the beginning of each week of the experiment, and (2) the number and kind of worms found post-mortem

in each animal. (Table 1.) Any gross pathological conditions found at necropsy have been noted, and the microscopical pathology of the liver and kidneys has been studied with a view to determining the action of the anthelmintics on these organs. Chemical analyses were made of the livers of representative sheep in order to determine whether copper is stored in the livers of sheep that receive copper sulphate solution. These results were checked by analyses of the livers of sheep not treated with copper sulphate solution. The effect of the different treatments on pregnant ewes and on the worm burden of lambs born of these ewes is presented.

TABLE 1.—*Number and kind of parasites recovered post-mortem from the experimental sheep*

Location and parasite	Number of parasites recovered when indicated weekly dose of anthelmintic was administered								
	100 c. c. of 1 per cent copper sulphate			5 c. c. of carbon tetrachloride		5 c. c. of tetrachlorethylene		None (controls not dosed)	
	Sheep 753[a]	Sheep 754[b]	Sheep 638	Sheep 738[c]	Sheep 761[d]	Sheep 744	Sheep 764	Sheep 762	Sheep 763
Esophagus:									
Gongylonema scutatum						4			
Abomasum:									
Haemonchus contortus	1		1				9	19	92
Ostertagia circumcincta	1		1	1	14		2	2	
Trichostrongylus extenuatus						1		6	117
Small intestine:									
Bunostomum trigonocephalum		6	10			3	1	11	61
Cooperia curticei	3			4	44			94	99
Nematodirus spathiger				53	7	1			
Trichostrongylus extenuatus									7
Trichostrongylus colubriformis	1		4	5	444		160		
Capillaria longipes	1			2	6				
Strongyloides papillosus	3			4	125	26	123		10
Large intestine:									
Trichuris ovis					2				
Oesophagostomum columbianum				15	191	1	18		24
Total	10	6	16	84	833	36	313	132	410

[a] Died Sept. 5, 1929, after about 50 weeks of treatment.
[b] Died Nov. 21, 1928, after about 4 weeks of treatment.
[c] Died June 22, 1929, after about 34 weeks of treatment.
[d] Died June 15, 1929, after about 33 weeks of treatment.

PARASITE EGG COUNTS

LOT RECEIVING COPPER SULPHATE

Sheep 753 had a relatively low egg count at the beginning of the experiment and continued with a low count throughout the experiment. This animal had no seasonal rise in egg count such as might have been expected from an infestation with species of parasites not amenable to the copper sulphate treatment. In the case of sheep 638, however, a seasonal rise took place between April 8 and May 27, the peak occurring on April 29. This animal had had a relatively high egg count on December 3, when it was placed in the experiment. After it had received two treatments with copper sulphate solution, the count dropped to a low level, and remained so during the rest of the experiment, except for the seasonal rise already noted.

Sheep 754 died from a colitis of undetermined origin four weeks after the experiment was begun. This animal had a low count during

this period and on post-mortem examination was found to have only six hookworms.

Lot Receiving Carbon Tetrachloride

Sheep 738 was only lightly infested at the beginning of the experiment, as shown by preliminary egg counts. This animal continued to have a low count up to the time of its death on June 22, 1929. No eggs were found for two weeks after it had had one treatment with carbon tetrachloride. For the three weeks following, only one egg per slide was found. The count then dropped to zero and remained there for 15 consecutive weeks, that is, between December 17, 1928, and March 25, 1929. However, this failure to obtain eggs with a

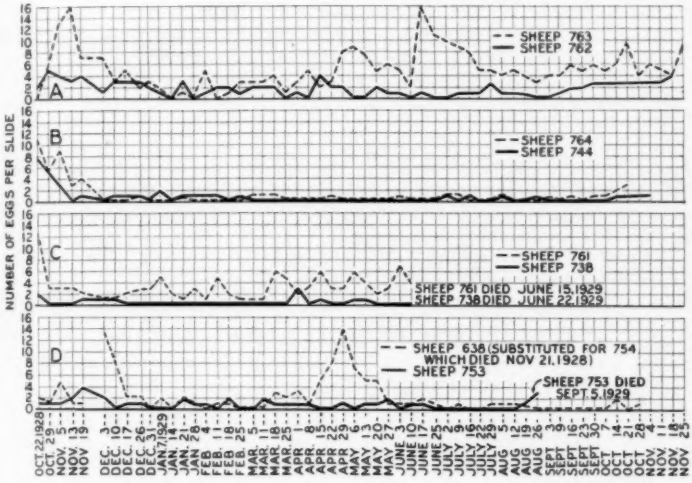

Figure 1.—Parasite-egg counts of sheep when untreated and when treated weekly with tetrachlorethylene, carbon tetrachloride, and copper sulphate in 1 per cent solution: A, Controls, no count on November 5, 1928, and no count or dosage on August 19, 1929; B, tetrachlorethylene treatment, no count on November 5, 1928, and no count or dosage on August 19, 1929; C, carbon tetrachloride treatment, no count on November 5, 1928, and no count or dosage on August 19, 1929; D, copper sulphate treatment, no count or dosage on August 19, 1929

dilution egg count can not be taken as prima facie evidence that an animal is free of parasites. It may mean that the parasitic infestation is so slight that eggs are not present in the feces in sufficient numbers to be detected in the great dilution used. This constitutes one of the objections to any method of dilution egg counting and renders necessary, in cases such as this, the employment of other methods as a check on the presence or absence of infestation.

In sheep 761, which had a relatively high count early in the experiment, the count was markedly lower after one treatment with carbon tetrachloride. It fluctuated considerably during the remainder of the experiment, but always remained considerably higher than that of sheep 738. The difference in the number of parasites found post-mortem, as shown in Table 1, clearly confirms the results of the egg counts in these two animals.

Lot Receiving Tetrachlorethylene

The most consistent results were obtained with the two animals treated with tetrachlorethylene. Both had a relatively high egg count at the beginning of the experiment. The reduction in number of eggs in the feces was not so rapid as in those of sheep 638, which received copper sulphate, or sheep 761, which received carbon tetrachloride. The egg count for sheep 744 reached a low level after three treatments with tetrachlorethylene; the count for sheep 764 reached a correspondingly low level after five treatments. From this point on, the results were very consistent, as both animals had low counts throughout the remainder of the experiment.

Although tetrachlorethylene did not bring about so rapid a destruction of nematode parasites in the sheep treated as did carbon tetrachloride in sheep 761 or copper sulphate in sheep 638, it nevertheless appears from the egg-count data that tetrachlorethylene, administered in weekly treatments for about a year, was more effective in controlling nematode infestation than were the other drugs used.

Control Lot

Considerable fluctuation occurred in the counts for sheep 763. The count reached a seasonal peak during the middle of June and continued at a relatively high level during the remainder of the summer and fall. The count for sheep 762 remained at a consistently lower level, a fact in keeping with the degree of infestation shown at necropsy. In the case of this latter animal there was no seasonal rise during the spring and summer when conditions are most favorable for the development of parasite eggs and larvae. Both control animals were of approximately the same age (3.5 years). Age resistance can not therefore be offered as an explanation of this apparent immunity to the heavier infestation which might be expected to occur, and usually does occur in the spring and summer. Individual susceptibility is suggested as a possible explanation for this difference in seasonal infestation.

PARASITES RECOVERED POST-MORTEM

Table 1 gives the number of parasites of different species recovered at necropsy from each animal in the experiment and the total number of parasites of all species found in each animal.

A comparison of the data in Table 1 with the egg-count data in Figure 1 indicates a close relationship between the worm burden, as demonstrated at necropsy, and the egg counts. In making such a comparison, one should bear in mind that the egg-producing capacity of some species of nematodes differs widely from that of other species. For instance, the females of *Haemonchus contortus* and *Bunostomum trigonocephalum* apparently produce eggs in far greater numbers than do the females of *Trichostrongylus* spp.

Treated Lots

The three animals treated with copper sulphate had very few parasites at necropsy, a finding which is in agreement with the egg counts for several weeks before death.

In the group receiving carbon tetrachloride, sheep 761, which had 833 parasites post-mortem, maintained throughout the course of the

test a considerably higher count than did sheep 738, which had 84 parasites post-mortem.

For both animals that received tetrachlorethylene the egg counts were consistently low. However, from September 3, 1929, to the close of the experiment, sheep 764, which had 313 worms post-mortem, had a higher count than did sheep 744, which had only 36 worms post-mortem. During the last two weeks of the experiment there was a marked increase in the number of eggs in the feces of sheep 764. This animal, a ram, fought repeatedly with the ram in the adjoining pen containing the control animals, and on October 10 broke through the fence and spent some time in the pen with the control sheep. It seems likely that during this time the animal acquired the Haemonchus infestation found at necropsy, and that the parasites developed to maturity between the last dosing on October 14 and the time of slaughter. The rise in the egg count during the last week of the experiment seems to substantiate this conclusion. For this reason, it is believed that a failure of the anthelmintic should not be charged with the responsibility for the presence of the specimens of Haemonchus present.

Control Lot

Sheep 763, which had the highest egg count most of the time during the experiment, had 410 worms on post-mortem examination, while sheep 762, which had a comparatively low egg count, had 132 worms on post-mortem examination. Both control animals had fewer worms post-mortem than did sheep 761, which was dosed with carbon tetrachloride, yet the egg count for sheep 763 remained generally higher than that for sheep 761. This is accounted for by the fact that sheep 763 was infested with considerable numbers of *Haemonchus contortus* and *Bunostomum trigonocephalum*, the females of which have a higher egg production than do the females of the small trichostrongyles which predominated in sheep 761.

DISCUSSION OF DATA ON EGG COUNTS AND PARASITES RECOVERED POST-MORTEM

From the data presented in Table 1, it is apparent that the animals receiving copper sulphate solution had fewer parasites post-mortem than did those receiving carbon tetrachloride or those receiving tetrachlorethylene. However, it can not be assumed from this that the copper sulphate solution was necessarily the most effective anthelmintic. It is obvious from the egg counts and the post-mortem findings for sheep 754, which died four weeks after the beginning of the experiment, that the sheep receiving copper sulphate had fewer parasites in the beginning than did the other groups, and that the relative freedom from parasites after treatment, therefore, was not necessarily attributable to the action of the anthelmintic.

Although it is not possible to determine the exact efficacy of the three anthelmintics used in the present experiment some conclusions may be drawn from the data here presented.

The copper sulphate treatment apparently controlled infestation with the stomach worm (*Haemonchus contortus*), as only one specimen was found in each of two animals and none in the third. The treatment failed to eliminate 6 and 10 hookworms (*Bunostomum trigonocephalum*), respectively, from two sheep, the third animal having no hookworms at necropsy. In the case of the small trichostrongyles,

no conclusions are warranted. From the post-mortem data on sheep 754, which may be considered a control animal as it died four weeks after the beginning of the treatment, it may be assumed that none of the animals in this group were heavily infested with trichostrongyles at the beginning of the experiment. Therefore, their absence on post-mortem examination can not be attributed with certainty to a high efficacy of the copper sulphate treatment against those trichostrongyles.

Carbon tetrachloride apparently completely controlled stomach-worm and hookworm infestation, but did not control the small trichostrongyles. In sheep 761, which had large numbers of these parasites post-mortem, the drug must be considered as having failed to eliminate them or even to keep them at a low level. What it did accomplish in preventing the worms from reaching still higher levels can not be ascertained from the experiment. In sheep 738 carbon tetrachloride seemed to be more effective against trichostrongyles in general but was not very effective against the thread-neck worm (*Nematodirus spathiger*), as this animal had a greater number of this species post-mortem than did any other; but here again no conclusion can be reached as to the extent of control.

Carbon tetrachloride had apparently little effect on nodular worms (*Oesophagostomum columbianum*). Sheep 761 had 191 nodular worms post-mortem, a large number compared with that found in other animals in the experiment. Sheep 738 had 15 nodular worms post-mortem, only slightly fewer than two of the other animals.

If the *Haemonchus contortus* infestation in sheep 764, for which a possible explanation has already been offered, is disregarded, tetrachlorethylene may be assumed to have controlled stomach worms and hookworms. In sheep 744 and 764 either the drug removed *Cooperia curticei* or there was no initial infestation with it. It controlled to some extent other small trichostrongyles in sheep 744. However, sheep 764 was moderately infested with *Trichostrongylus colubriformis* and *Strongyloides papillosus*. The drug may have controlled nodular worms in sheep 744 but was apparently not very successful in this respect in sheep 764.

POST-MORTEM PATHOLOGY

In order to determine the effect of the various treatments on the sheep, a careful study was made at necropsy of the gross and microscopical pathology. Four animals died before the completion of the experiment. Two of these had been dosed with copper sulphate solution and two with carbon tetrachloride. The pathological findings for these four animals and for those that were slaughtered at the termination of the tests follow.

Sheep 754, treated with copper sulphate, died during the night of November 21, 1928, about four weeks after the beginning of the experiment. The attendant stated that for several days before it died this animal had shown symptoms of illness and was affected with a severe diarrhea. The heart appeared normal except for a fibrosis and thickening of the left bicuspid valve; the lungs were edematous; the small intestine was congested, slightly inflamed, and petechiated; the colon was inflamed. The large colon was thickened and contained numerous nodules, yellow diphtheritic patches covered the mucosa, and there were numerous ecchymoses. No other lesions were present. The cause of death was evidently a colitis of undetermined origin.

Sheep 753, treated with copper sulphate, was reported dead on September 5, 1929, after having been in the experiment about 45 weeks. This animal appeared weak when dosed on August 26 but was still eating and apparently not ill. The attendant reported that it subsequently refused to eat, developed a diarrhea, and finally assumed a position of decubitus. The abomasum contained one small area, 2.5 cm. in diameter, which was inflamed and slightly eroded but was otherwise normal. This lesion may have been due to decomposition. The small intestine was stained with bile and slightly inflamed. The caecum contained a diverticulum with an opening 2.5 cm. in diameter, the pouch being large enough to hold a walnut. The small intestine, caecum, and colon contained numerous nodules caused by the larvae of *Oesophagostomum columbianum*. The liver contained numerous tracts of old cicatricial tissue and numerous raised necrotic areas 1 to 2.5 cm. in diameter, with semicaseous centers. G. T. Creech, of the pathological division of the bureau, examined the liver and expressed the opinion that the lesions were due to *Actinomyces necrophorus*. Decomposition was too far advanced to warrant culturing the material.

Sheep 738 and 761, treated with carbon tetrachloride, began to show symptoms of emaciation and debility about February 15, 1929. The animals were failing to clean up the feed. As time went on their condition became gradually worse until there was pronounced weakness, emaciation, and loss of appetite. Sheep 761 was found moribund on June 15, 1929, and was killed. The carcass was extremely emaciated, the muscular tissue soft, flabby, and infiltrated with watery fluid. The peritoneal and pleural cavities each contained about 250 c. c. of watery fluid. All fat in the body was soft and gelatinous. The lymph glands were soft, edematous, and surrounded by watery fat. The heart muscle was pale and flabby. The lungs were edematous; the liver had a greasy appearance; the spleen was soft and pulpy; and the kidneys were soft, pale, and flabby. The rumen had numerous raised, whitish blisters which were particularly abundant around the esophageal groove. The surface was roughened and contained red, eroded, ulcerlike foci and old scars of previous erosions. The musculature of the fourth stomach and intestinal tract was pale and edematous.

Microscopical examination of the liver showed a small amount of fatty infiltration in the vicinity of the central vein and slight chronic interstitial hepatitis. The kidneys were apparently normal.

Sheep 738, treated with carbon tetrachloride, died on June 22, 1929. This animal was caught out in a severe thunderstorm and was too weak to get under cover. The carcass was emaciated but not so extremely so as that of sheep 761. The muscular tissue was pale and flabby and infiltrated with a watery fluid. The abdominal fat and the mesentery were gelatinous and watery. The thyroids were greatly enlarged, measuring 9 by 4.5 cm. The rumen showed the same blistered condition as that of sheep 761. An area extending downward 15 cm. from the esophageal groove and 30 cm. in length contained reddish, swollen blisters 2 cm. in diameter, infiltrated with smaller blisters or erosions 1 to 2 mm. wide with open, craterlike centers. Between these areas were eroded foci of scar tissue, some of which were deep purple and evidently necrotic. The lungs were edematous and congested; the heart muscle was pale and flabby. The spleen

pulp was thin and watery. The hilus of each kidney was watery and gelatinous. The liver appeared to be atrophied, weighed 344 gm., and contained small necrotic foci 2 to 4 mm. in diameter. The small intestine, caecum, and colon contained numerous calcareous nodules.

Microscopical examination of the liver showed slight hyperemia and fatty infiltration of cells in a few areas. In the kidney which was examined a slight chronic interstitial nephritis was found.

Sheep 638, treated with copper sulphate, was slaughtered on October 29, 1929. The carcass was in excellent condition and contained a large quantity of fat. The heart had extensive deposits of fat in the region of the left auricle. The lungs contained grayish, slightly raised areas, evidently due to the presence of lungworms of the genus Muellerius. The liver had on the surface five calcareous areas 5 to 15 mm. in diameter. There were numerous furrows and areas of scar tissue, evidently due to previous parasitic invasion. The kidneys were congested. The abomasum was slightly congested, with two small punctiform hemorrhages on the greater curvature. The small intestine, caecum, and colon contained numerous calcareous nodules.

Microscopical examination of the liver revealed slight hyperemia, a small amount of round-cell infiltration in the vicinity of some vessels, and slight fatty degeneration. Examination of the kidneys revealed a slight chronic interstitial nephritis and slight hyperemia.

Sheep 744, treated with tetrachlorethylene, was slaughtered on November 5, 1929. The animal was in excellent condition. One lung contained a large caseated raised area 8 mm. in diameter and some small nodules. The liver contained a large calcified area 1 cm. in diameter. Examination of the kidneys showed chronic interstitial nephritis. The rumen contained, near the middle of the right longitudinal groove, a pedunculated papilloma extending for 5 cm. above the mucosa and ending in a roughened, rounded protuberance. Numerous calcareous nodules were present in the intestinal tract.

Microscopical examination of the liver showed perivascular round-cell infiltration and slight hyperemia. The kidney which was examined had chronic interstitial nephritis, glomerulo-nephritis with infiltration of leucocytes, and thickening of glomerular capsule.

Sheep 764, treated with tetrachlorethylene, was killed on October 21, 1929. The animal was last dosed on October 14. The lungs showed anthracosis, and the liver contained small areas of fibrosis 1.5 cm. in diameter. No other lesions were present.

Microscopical examination of the liver revealed focal round-cell infiltration with marked eosinophilia. Other areas, walled off by round cells and spindle cells, contained seminecrotic centers of degenerated eosinophiles surrounded by foreign body giant cells, the lesions being apparently due to parasitic invasion. Examination of the kidneys showed hyperemia, a slight chronic interstitial nephritis, and hemorrhages in glomeruli.

Sheep 762 (control), was killed on November 18, 1929. Numerous dull-red punctiform hemorrhages were present on the mucosa of the abomasum. The small intestine contained numerous nodules and bright-red punctiform hemorrhages. Calcareous nodules were very numerous in the large intestine.

Microscopical examination showed that the liver was apparently normal and that the kidneys had a slight chronic interstitial nephritis

Sheep 763 (control) was slaughtered on November 25, 1929. The mucosa of the abomasum contained numerous dull-red punctiform hemorrhages. Bright-red punctiform hemorrhages were present in the small intestine. There were numerous calcareous nodules in the caecum.

Microscopical examination revealed focal round-cell infiltration and a small amount of fatty infiltration in the liver and slight chronic interstitial nephritis in the kidney.

DISCUSSION OF PATHOLOGICAL FINDINGS

It will be seen that the microscopical study of sections from the livers and kidneys of the sheep failed to show any lesions that might be directly attributed to the action of the respective drugs. Lesions such as fatty infiltration and round-cell infiltration of the liver and chronic interstitial nephritis found in some of the treated animals were also present in the control animals. This fact, therefore, rules out the likelihood that lesions of this type were caused by the action of the anthelmintics used.

The absence of severe liver lesions in the sheep that received carbon tetrachloride is surprising in view of the fact that the drug commonly produces central necrosis in the liver of the dog, and that in the experiments of Wright (*16*) single doses of 10 and 20 c. c. administered to sheep have been followed by central necrosis in the liver. Evidently the organ is capable of adjusting itself to the action of the drug when it is given in repeated weekly doses.

The generalized edema found in both of the animals that received carbon tetrachloride was apparently not due to liver, kidney, or heart lesions. The chronic interstitial hepatitis found in the liver of sheep 761 was apparently not of sufficient extent to cause circulatory disturbances; the kidneys of this animal seemed to be normal. The liver of sheep 738 contained no lesions that would cause circulatory interference. The writers believe that the slight chronic interstitial nephritis could not have been responsible for the edema. In view of the absence of other contributory lesions, it is possible that the continued absorption of carbon tetrachloride over a long period of time may have had a damaging effect on the walls of the blood vessels, weakening them to such an extent as to bring about the condition of generalized edema found at necropsy. Such injury may have been due to the direct action of the drug on the endothelial cells of the capillaries or it may have resulted from changes in blood chemistry after repeated administration of the drug. The precise explanation of the edema would require a special investigation.

Although the deaths of the sheep receiving carbon tetrachloride can not be attributed directly to any lesion or set of lesions found at necropsy, it is apparent that the repeated weekly administration of the drug was responsible in some way for circulatory disturbances and possibly digestive disturbances, as indicated by the partial anorexia that was shown by both animals for approximately four months before death. The lesions found in the rumen of both animals may have contributed to the loss of appetite and the condition of general debility.

The absence of liver and kidney lesions attributable to the anthelmintic in the sheep receiving tetrachlorethylene is not so noteworthy as the absence of such lesions in the animals receiving carbon tetrachloride. Schlingman and Gruhzit (*13*) found fatty infiltration and

degeneration in the livers of sheep given tetrachlorethylene in doses of 5 to 20 c. c. (0.22 to 0.833 c. c. per kilogram of weight), but concluded that the organs of sheep seem to have considerable tolerance for the drug. The results in the present case support their conclusions. Lamson, Robbins, and Ward (*9*) could find no pathological changes in the livers of dogs given various doses of tetrachlorethylene.

COPPER CONTENT OF SHEEP LIVERS

In order to determine whether copper is retained in the liver after the administration of copper sulphate solution, chemical analyses were made of the livers of the sheep treated with copper sulphate, of the livers of the control sheep, and of the liver of one animal receiving tetrachlorethylene.[3] The results are reported in Table 2. Analyses were also made of the livers from five lambs that had received four doses of copper sulphate and nicotine sulphate at monthly intervals in an experiment conducted by the animal husbandry division of the bureau.

TABLE 2.—*Copper content of livers of sheep treated with copper sulphate solution and of those not treated with copper sulphate solution*

Sheep No.	Quantity of anthelmintic and method of treatment	Quantity of copper found in liver
		Per cent
753	100 c. c. copper sulphate once weekly for 42 weeks	0.030
638	100 c. c. copper sulphate once weekly for 52 weeks	.060
762	None. (Control)	.005
763	do	.003
744	5 c. c. tetrachlorethylene once weekly for 53 weeks	.003
1	1 c. c. of a 1 per cent solution of copper sulphate and nicotine sulphate, per pound of weight, given on July 3, Aug. 7, Sept. 4, and Oct. 16; animal killed Nov. 12.	.009
2	do	.009
3	do	.006
4	do	.008
5	do	.009

Copper is apparently normally present in small quantities in the livers of some animals. The authors have been unable to find in the literature any reference to determinations of copper in the liver of sheep, but Powick and Hoagland (*12*) found the average copper content of 9 fresh ox livers to be 0.0039 per cent, of 6 fresh calf livers to be 0.0045 per cent, and of 6 fresh hog livers to be 0.0004 per cent.

The data indicate that the livers of the sheep that received copper sulphate solution weekly contained approximately ten times as much copper as the livers of sheep that did not receive the copper sulphate solution. About four weeks after the last treatment the copper content of the livers of the five lambs that received four doses of copper sulphate at monthly intervals was approximately twice as great as that of the livers of the untreated animals. These analyses indicate that after the administration of copper sulphate copper is stored in the liver of sheep and the accumulation persists for some time.

The results of the analyses of the livers of untreated sheep shown in Table 2 are in close accord with those of Powick and Hoagland for ox and calf livers. These findings are of interest in connection with

[3] These analyses were made by Jacob M. Schaffer, of the biochemic division of the bureau.

investigations in progress in various parts of the world on the relations of copper salts and liver to anemia.

The copper analyses were also undertaken to determine whether the continued dosing with copper sulphate solution might have accounted for the liver lesions found in sheep 753, which died during the course of treatment. The liver of this animal had a copper content of 0.03 per cent, whereas the liver of sheep 638 had a copper content twice as great. The latter animal was dosed for a longer period and was in good health when killed, the liver being apparently normal. Polson (*11*) reported no detrimental effects in rabbits and guinea pigs from feeding relatively large quantities of copper acetate for considerable periods of time. The writers believe that the dosing with copper sulphate was not in any way responsible for the death of sheep 753.

EFFECT OF ANTHELMINTICS ON PREGNANT EWES AND ON THE WORM BURDEN OF THE OFFSPRING

As previously stated, four of the ewes in this experiment were pregnant at the beginning of the tests. The lamb from sheep 738 was born on the night of February 15, 1929, and weighed 8 pounds (3.6 kgm.) on February 18. This animal was not strong and succumbed on February 26, probably from exposure to severe weather which prevailed at that time.

The lamb from sheep 761 was born on the night of February 16, was strong and vigorous, and weighed 10.5 pounds (4.8 kgm.) on February 18.

The lamb from sheep 744 was born on the night of February 18. The weather was very cold, and the lamb died the following morning from congenital weakness and exposure.

The lamb from sheep 638 was born on February 22, and weighed 12 pounds (5.5 kgm.) on February 25.

There is no evidence to indicate that the weekly dosing was in any way responsible for the fact that sheep 738 and 744 produced weak lambs. Sheep 738 was dosed with carbon tetrachloride as was sheep 761, which produced a strong, vigorous lamb. This fact eliminates the possibility that the drug might have been a factor in the congenital weakness of the lamb born of sheep 738. Sheep 744, which was dosed with tetrachlorethylene, at no time reacted to repeated treatment with this drug and was in excellent physical condition when slaughtered at the termination of the experiment. There is no reason to believe that the treatment reacted in any way on the intrauterine development of the lamb.

Lambs 761 and 638 [4] were raised to maturity. They were kept in the pens with their mothers until the close of the experiment, November 25, 1929, at which time lamb 761 weighed 70.5 pounds (32 kgm.) and lamb 638, 69 pounds (31.4 kgm.). Lamb 761 became heavily infested with ticks about April 1, 1929, and was dipped several times in a 1 per cent cresol solution. Lamb 638 sustained a complete fracture of the right metacarpus on September 5, 1929. The fracture was reduced and a cast applied to the leg, and the lamb recovered.

The feces of the lambs were examined weekly for parasite eggs. Eggs of Strongyloides appeared in the feces of lamb 761 on March 11,

[4] The lambs have been designated by the numbers assigned their mothers in order to indicate the lots in which they were kept.

1929, and by the following week they were very numerous. At this time the lamb suffered from a slight diarrhea, which was apparently due to the Strongyloides infection. Coccidia appeared in the feces of lamb 638 on April 15 and in the feces of lamb 761 on May 6. The coccidia were not numerous and apparently caused no clinical symptoms.

The first strongyle egg appeared in the feces of lamb 761 on May 13 and in the feces of lamb 638 on June 17. Beginning on July 9, counts were made weekly of the eggs in the feces of these lambs. These counts are plotted in Figure 2. It will be seen that these lambs at no time showed evidence of heavy infestation with strongyles, but that the counts were uniformly light until the termination of the experiment. In view of the fact that lambs kept on small areas with parasitized sheep are usually heavily infested with parasites and frequently succumb to such infestations, it must be concluded that the repeated anthelmintic treatment of the adult animals resulted in a reduction of the infestation in the pens and a consequent light infestation in the lambs.

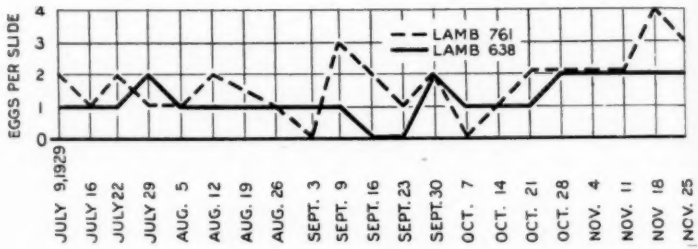

FIGURE 2.—Parasite-egg counts of the lamb from sheep 761, treated with carbon tetrachloride, and the lamb from sheep 638, treated with copper sulphate solution. No egg counts were made August 19

GENERAL DISCUSSION

In general, the egg counts indicate that in those animals that had a relatively high infestation at the beginning of the experiment, the infestation was reduced to a minimum within three to five weeks and remained at a relatively low level during the rest of the experiment. A single exception occurred in the case of one animal that received copper sulphate solution. This animal had a seasonal rise in the egg count during the spring months.

From the evidence presented by the egg counts and by the number of parasites recovered post-mortem, it may be concluded that a 1 per cent solution of copper sulphate controlled infestations with the stomach worm (*Haemonchus contortus*), but failed in two instances to remove hookworms (*Bunostomum trigonocephalum*). No conclusions are possible in the case of the small trichostrongyles, as the sheep that received copper sulphate were apparently only lightly infested with these parasites at the beginning of the experiment.

Carbon tetrachloride apparently removed stomach worms and hookworms. In sheep 761, the drug must be considered as having failed to control infestation with small trichostrongyles and nodular worms (*Oesophagostomum columbianum*) to a satisfactory degree; it may have prevented more serious infestations with these worms. In sheep 738, carbon tetrachloride seemed to be somewhat more effective

against small trichostrongyles but failed to reduce the number of thread-necked worms (*Nematodirus spathiger*) to a satisfactory extent. In this animal the drug apparently had little effect on nodular worms.

Tetrachlorethylene did not reduce the initial worm burden so rapidly as did copper sulphate solution or carbon tetrachloride. However, tetrachlorethylene gave the most consistent results. The egg counts of the two sheep that received this anthelmintic indicated a negligible degree of infestation after three and five weeks, respectively, and remained at a very low level during the course of the experiment. The drug apparently controlled stomach worms and hookworms and may have removed *Cooperia curticei;* initial infestation with this worm may or may not have been present. In sheep 744 tetrachlorethylene apparently controlled to a considerable extent infestations with other small trichostrongyles but was not so successful in this respect in sheep 764. The drug may have had some effect on nodular worms in one animal but failed to control these parasites very satisfactorily in the other.

In no case was it possible with any of the anthelmintics to remove all parasites. It is probable that the small trichostrongyles in the fourth stomach and the small intestine are covered by a sufficient amount of mucus and débris to be protected from the action of the anthelmintics tested when they are introduced into the gastrointestinal tract. None of the anthelmintics used in this experiment was entirely effective in removing these worms, and it is apparent that either some other mode of attack must be resorted to or that other remedies must be devised which will penetrate to the parasites or exert a more powerful action upon them.

In regard to the safety of the various anthelmintics, it will be recalled that two animals receiving copper sulphate solution died before the termination of the experiment. However, the death of these animals can not be attributed to the repeated administration of copper sulphate. One animal apparently succumbed to a colitis after having had only five weekly treatments and the other to a liver condition resembling an infection with *Actinomyces necrophorus.* A chemical analysis showed that the liver of the latter animal contained only half as much copper as did that of the animal surviving a year's treatment with copper sulphate.

Chemical analyses indicate that in the livers of sheep treated weekly for a year with copper sulphate the amount of copper present was approximately ten times as great as that in the livers of untreated sheep, and that the accumulation of the copper persisted for some time. The livers of animals that received four doses of copper sulphate at monthly intervals contained approximately twice as much copper as those of untreated sheep.

The administration of carbon tetrachloride weekly for 33 and 34 weeks, respectively, apparently caused the deaths of the two animals treated. The animals showed anorexia, progressive loss of weight and condition, and general debility. At necropsy, the two sheep were found to have a generalized edema and lesions in the rumen probably resulting from local irritation caused by carbon tetrachloride. The deaths of these animals can not be directly attributed to any lesion or set of lesions found at necropsy. However, it is apparent that the repeated weekly administration of the drug was responsible for circulatory and digestive disturbances. In view of the absence of any material lesion

of the heart, kidneys, and liver of the treated animals, the exact manner in which the drug produced these disturbances is not understood. Tetrachlorethylene was very safe; no deleterious results followed its prolonged administration, and the animals maintained good health and condition during the entire course of the experiment. No postmortem lesions attributable to the action of the drug were found.

Two of the lambs born of ewes in the experiment died of exposure or congenital weakness; the others made good growth and, although kept on the same ground without treatment, had only a small worm burden throughout the course of the experiment. It is apparent that the repeated anthelmintic treatment of the older animals in the same lots had the effect of controlling parasites in the lambs.

SUMMARY AND CONCLUSIONS

Weekly treatments for a little more than a year with 100 c. c. of a 1 per cent copper sulphate solution, 5 c. c. of carbon tetrachloride, or 5 c. c. of tetrachlorethylene failed to remove all parasites present in sheep kept in small inclosures. Tetrachlorethylene gave the best results and produced no bad effects.

Although total elimination of parasites was not possible, repeated anthelmintic treatment resulted in greatly reducing the worm burden of the sheep and maintaining it at a low level during the experiment.

Two sheep receiving carbon tetrachloride died in 33 and 34 weeks, respectively, after the experiment was begun, apparently from the effects of repeated administration of the drug. It is therefore apparent that sheep can not be safely treated once every week with carbon tetrachloride.

The weekly administration of tetrachlorethylene or 1 per cent copper sulphate solution caused no harm to the sheep in this experiment.

Pathological changes in the livers and kidneys of the treated sheep could not be attributed to the action of the various anthelmintics.

Chemical analyses of sheep livers indicate that there is a considerable storage of copper in the organ following the administration of copper sulphate solution. This storage apparently was not responsible for the production of toxic symptoms, and copper sulphate was found not to act as a cumulative poison.

The repeated anthelmintic treatment with each of the drugs did not cause abortion in pregnant ewes. Lambs born of ewes in the experiment maintained a consistently low level of parasitic infestation, though untreated and kept on the same ground with the ewes.

The results of the experiment answer conclusively the questions which led the writers to undertake the present work. These results indicate that the attack against parasites of sheep must be directed along lines in which the factor of degree of stocking on pastures is definitely taken into consideration and correlated with the factor of medicinal control. Combining the use of larger areas with weekly treatments with drugs which, in this paper, have been shown to be safe for sheep may result in eradication of the parasites.

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AN APPARATUS FOR GROWING PLANTS UNDER CONTROLLED ENVIRONMENTAL CONDITIONS[1]

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INTRODUCTION

The discovery by Garner and Allard (*6*)[2] of the day-length response of plants established definite need for an installation which would make possible a study of the effect of length of day with accurate control of other variable factors incapable or difficult of control outdoors. Among these factors were light, temperature, humidity, air velocity, and soil moisture (*13*).

Possibly the greatest handicap hitherto has been the inability to supply constant illumination of sufficient intensity and the required quality to enable the plant to complete its full life cycle. With the continued improvement in artificial sources of light during the past century repeated efforts have been made to utilize them in experimental work.

The recent publication of methods for using the gas-filled tungsten-filament lamp by Harvey (*8*), the Boyce Thompson Institute for Plant Research (*2, 3*), Maximow (*12*), Lundegärdh (*11*), Truffaut and Thurneyssen (*14*), and Davis and Hoagland (*5*) indicates that the interest in this method of experimentation has greatly increased. There is apparently a real need for suitable equipment for growing plants under accurately controlled conditions. Moreover, it is not impossible that the future development of light sources of much higher efficiency than present types (only about 2.5 to 10 per cent) will permit of the commercial utilization of artificial light in some phases of agriculture. It seems desirable, therefore, to publish a brief description of the apparatus developed for study of the day-length response of plants under controlled environmental conditions. The experience gained with the equipment during more than a decade is essentially of an engineering nature and should prove of service to those designing or using similar installations. It was found necessary to design and develop new types of equipment and methods for the control of humidity, soil moisture, and illumination.

CONTROL OF LIGHT

The plants are grown in light-proof cabinets or "light cases." These cases were designed with certain requirements in mind. They must, in view of cost of operation and space requirements, be small. In order to avoid daily handling of the plants, a separate and independent unit should be provided for each lot of plants subjected to different treatment. The units should be so constructed as to permit their use in a lighted room. They should permit of accurate tempera-

[1] Received for publication July 11, 1931; issued January, 1932.

[2] Reference is made by number (italic) to Literature Cited, p. 1084.

ture and humidity control by ventilation with a constant volume of conditioned air. Lastly, by far the most important and exacting requirement is the efficient utilization of the light of the illuminant with the least disturbance in air temperature about the plants.

Various minor changes have been made in the design of the light case as information gained through use since 1919 has accumulated.

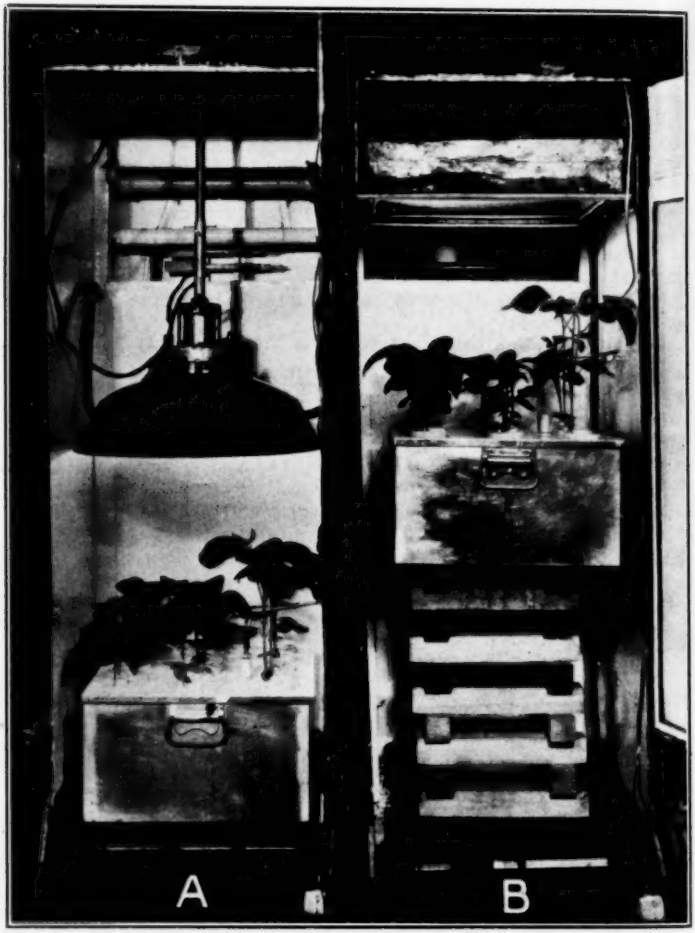

FIGURE 1.—Interiors of two light cases equipped with globular water screen (A) and with tray water screen (B). (See text)

The present unit (fig. 1) consists of a galvanized-iron box 20 inches wide, 24 inches deep, and 78 or more inches high. A false partition, 4 inches from the back, serves to make the case vertically symmetrical and forms a discharge duct for ventilation. At the front is a door,

almost the full height and width of the case, which may have, if desired, a glass and shutter. An opening in the bottom of the door serves as an air inlet. The top of the case, from which the lamp and reflector are suspended, is perforated to permit air to be drawn over the base of the lamp. The outlet, or vent, for ventilation of the lower part of the compartment, where the plants are placed, is in the false partition just below the water screen. Another opening, just above the water screen, ventilates the upper part of the compartment, where the lamp is placed. The duct into which both vents open has a damper which regulates the quantity of air passing through the case.

In the apparatus used until recently there is interposed between the lamp and the plants an open pan with glass bottom, through which water constantly flows. (Fig. 1, B.) The use of this type of water screen is not without objection on account of the deposition of sediment and the growth of algae in the trays, with consequent diminution in light intensity. This difficulty can be overcome to some extent, however, by the use of distilled or soft water with recirculating pump and refrigeration. Another alternative is the use of a water-softening apparatus and filter for treating the tap water before use. In the present instance, neither of the above arrangements has been used. The tap water was not treated in any manner except that it was kept at a constant temperature slightly above the dew point of the air in the cases to prevent fogging of the glass. The trays were cleaned weekly or oftener to remove all sediment. This requires about five minutes per case, the light being off about three minutes. Use of special glass opaque to infra-red radiation is possible but only with a large loss and alteration in color of the transmitted light. Recently a new and superior type of water screen has been installed. (Fig. 1, A.) Its details are referred to later.

The interiors of two light cases are shown in Figure 1. One (A) is equipped with globular water screen, water-cooled lamp, and reflector; the other (B), with tray water screen, having the lamp and reflector above. Adjustment in distance between lamp and plant is by means of the supporting screw in case A and by wood blocks under the plant container in case B. The plant containers rest on tared balances with beams having electrical contacts. The electrical plugs in front of the balances (air inlet) are for the fixed heaters that compensate for the drop in air temperature caused by the water screen when the lamp is off. The recording and indicating instruments in the back are in the air vents of the cases. The tubes projecting from the right-hand side of the cases are for automatic addition of water to the soil in the containers. In each container are three varieties of soybeans 2 weeks old.

Within reasonable limits, illumination intensities attainable with the gas-filled tungsten lamp used in conjunction with the tray water screen are not limited by lamp size but by the heat generated and the arrangements made to prevent injury to the plants and case. Protection of the top of the case is unnecessary with lamps up to 2,000 watts in size, if ventilation is at the rate of 50 cubic feet of air per minute. Lamps totaling even as much as 4,000 watts per case have been used with no injury except the melting of the solder at the top of the case. Where protection for the case is necessary, the simplest arrangement is the use of a ring nozzle to flow water over the outside of the reflector.

When a 1,000-watt 110-volt lamp in a deep-bowl porcelain-enameled reflector is used, the average illumination immediately below the tray is about 4,200 foot-candles. This intensity was determined by ruling off the water screen into squares, determining the intensity in the center of each square with a Macbeth illuminometer, and averaging the results. The distance from the light center of the lamp to the bottom of the water screen (containing a 3-inch layer of water) was 8½ inches. Since the lamp is rated at 20,100 lumens and only 7,500 lumens (area of glass in square feet × 4,200 foot-candles) get through the water screen, the efficiency of utilization is 37 per cent. A bowl-frosted lamp gave slightly lower illumination values without any marked improvement in evenness of distribution.

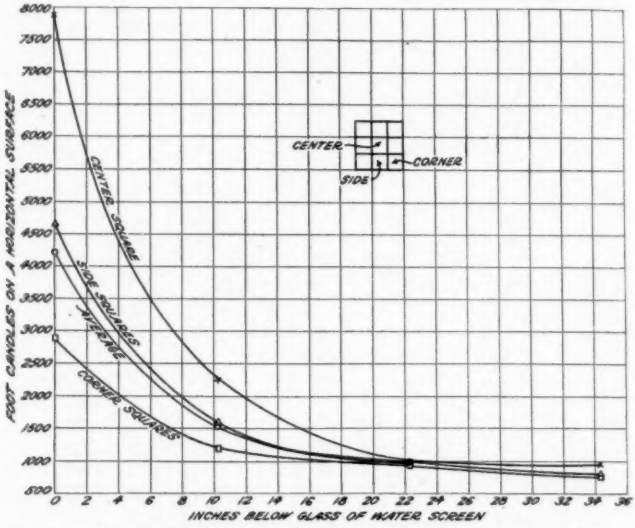

FIGURE 2.—Illumination intensities in the plant compartment of light case having a 1,000-watt 110-volt gas-filled tungsten lamp and a tray water screen with a 3-inch depth of water. To convert foot-candles to approximate gram calories per square centimeter per minute, divide by 6,000

Figure 2 shows the distribution of light in cases having tray screens. The conversion value (6,000 foot-candles = 1 gram-calorie per square centimeter per minute) was determined with a pyranometer (*1*).

Uniformity of light distribution immediately below the tray water screen is not satisfactory but improves rapidly with increasing distance below the screen. If the water screen is assumed to have been ruled off into nine equal squares, the ratio of the intensity at the corner square to that at the center square is 1:2.6 at the glass, 1:1.7 at 10 inches below the glass, and 1:1 at 22 inches below the glass. Without a special reflector, greater horizontal uniformity can be obtained only by using a large number of small lamps and wasting much of the light or by using larger cases and more lamps. For example, it was found that with four 1,000-watt 220-volt lamps in an improvised galvanized-iron reflector the ratio of corner to center intensity was 1:1.75 next to the glass and 1:1.43 at 6 inches from the glass. Incidentally the average illumination next to the glass,

with the reflector freshly painted with aluminum bronze, was about 8,100 foot-candles.

The lighting equipment has been improved recently in many respects by the use of water-cooled lamps (fig. 3) having globular water screens, of a type similar to that recently described by Gordon (7). The lamps burn immersed in stagnant distilled water which is kept cool by a copper coil through which cold tap water circulates. In designing these units, especial care was taken to provide efficient heat absorption by the use of a layer of water 3 inches thick and a cooling coil of maximum size. The arrangement of the stuffing box that fits around the neck of the lamp has been designed to permit renewal of the lamp bulb from below without dismounting and disassembling the entire unit. (Fig. 4.) The units require the use of gas-filled tungsten lamps in special bulbs designated by the manufacturers as T–20 Kl.

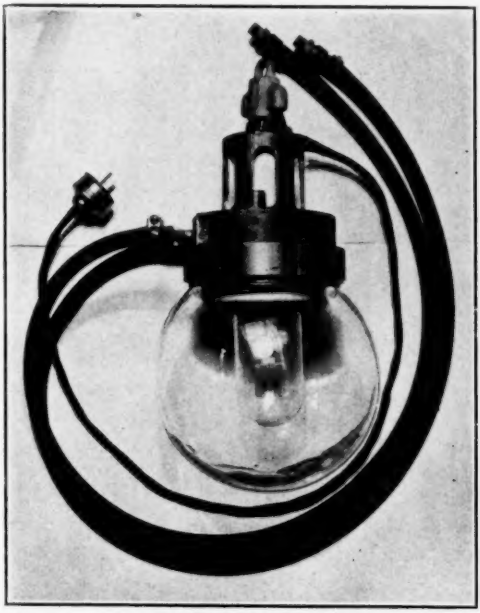

FIGURE 3.—Water-cooled lamp with reflector removed. The space between the lamp and the surrounding globe contains distilled water which is cooled by circulation of cold tap water through the coil around the top of the lamp

The use of the globular water screen has several advantages over that of the tray or flat screen. Most important is the fact that the water remains clear and that the light does not alter in intensity or quality because of the presence of sediment or algae. Another marked advantage is the much higher lighting efficiency achieved, 62 per cent as compared to 37 per cent with the trays. The light distribution is also greatly improved, since with the trays the illumination at 12 inches from the light center of the lamp is 2,650 foot-candles ±57 per cent, while with the globes it is 2,609 foot-candles ±26 per cent. The distribution of illumination in a light case having a 1,000-watt 110-volt water-cooled lamp with porcelain-enamel dome reflector is plotted in Figure 5.

The use of the water-cooled lamp makes it possible to raise and lower the lamps instead of the plants. This is accomplished by means of a slotted screw which is worked up and down by means of two bevel gears and a crank outside the light case. The lamp travel is 45 inches. The water connections to the lamp are of

rubber hose. This arrangement minimizes injury to the plants, since they need not be raised or lowered during the experiment.

The rise in air temperature in the light case with a 1,000-watt 110-volt water-cooled lamp can be kept down to 1.6° F. if fairly cold tap water is available.

There is, according to the lamp manufacturer, no essential difference in quantity and quality of light between the 1,000-watt 110-volt lamp in the standard PS-52 bulb, used with the tray screens, and the T–20 Kl bulb, used with the globular screens. Both lamps are rated at 20,100 lumens and burn at a color temperature[3] of 3,000° K.[4] Moreover, both types of screen use a 3-inch depth of water and a glass envelope about one-eighth of an inch in thickness. The glass envelopes are made of a somewhat greenish glass and probably have approximately the same transmission. For these reasons it is not unreasonable to assume that, within the limits of accuracy in manufacture, the same spectral radiation is obtained with both types of unit.

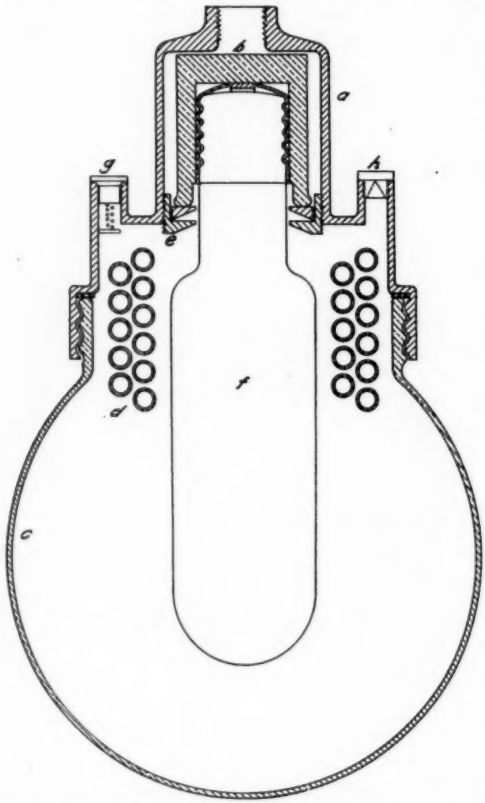

FIGURE 4.—Details of construction of the water-cooled lamp: *a*, bronze canopy; *b*, porcelain lampsocket; *c*, glass globe; *d*, copper cooling coil; *e*, bronze stuffing box; *f*, tungsten lamp; *g*, pop valve; *h*, filler

The data plotted in Figures 6 and 7 are believed applicable to both tray and globe equipment. The coefficient of transmission of window glass and that of water are known, as are also the spectral distribution of solar radiation and the relative visibility of radiation; these data have been used in the computation of the curves. The lamp radiation was computed by means of Planck's equation for a black body at 3,000° K.

[3] The temperature of a black body at which its color matches a given radiation is known as the "color temperature" of that radiation.

[4] The Kelvin, or absolute, scale of temperature.

While it is not claimed that these curves are highly accurate, they nevertheless serve to illustrate the differences between solar radiation and the artificial illumination utilized. These differences are more clearly brought out in Table 1. Solar light was computed at 54 per cent short-visible and 46 per cent long-visible radiation; that of the water-cooled lamp as 29.5 per cent short-visible and 70.5 per cent long-visible radiation. According to Luckiesh (*10*), the percentage distribution of radiation from the tungsten lamp itself is: Ultra-violet, 0.2; visible, 13.6; infra-red, 86.2.

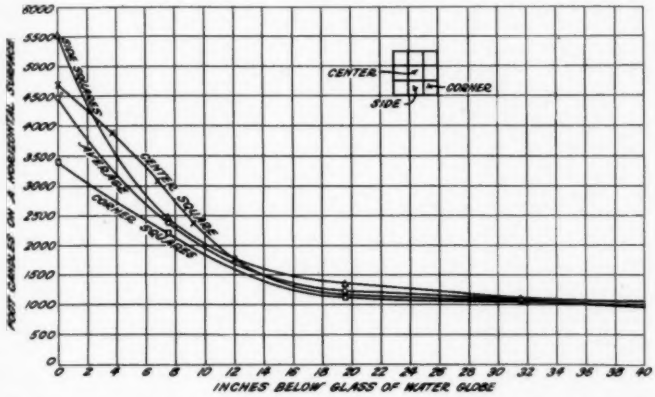

FIGURE 5.—Illumination intensities in the plant compartment of light case having a 1,000-watt 110-volt gas-filled tungsten lamp and a globular water screen with a 3-inch depth of water. To convert foot-candles to approximate gram calories per square centimeter per minute, divide by 6,000

TABLE 1.—*Spectral distribution of the radiation from the sun and from the water-cooled lamp*

Spectral region	Wave length	Radiation from—	
		Sun	Water-cooled lamp
	μ	*Per cent*	*Per cent*
Ultra-violet	0.30 to 0.40	2.2	0.7
Short visible	.40 to .58	26.8	15.4
Long visible	.58 to .76	22.9	37.1
Infra-red	.76 to ∞	48.1	46.8
Total	.30 to ∞	100.0	100.0

Except by means of a water screen to decrease the infra-red radiation from the lamp, no attempt has been made to overcome the discrepancies between the radiation from the water-cooled lamp and sunlight. Changing the color of the light to coincide with sunlight, although feasible, is not practicable in this case, inasmuch as it would require the use of a 6,000 to 8,000 watt lamp to supply the desired light intensity. Moreover, no attempt has been made to supplement the deficiencies of the tungsten lamp in the ultra-violet and short-visible radiation.

The luminous efficiency of the screened-lamp radiation was found to be 6,000 foot-candles per gram calorie. This value is quite comparable to the value of 6,720 foot-candles for sunlight (air mass 1.1) determined by Kimball (*9*). The value computed from the light curves of Figure 7, uncorrected for the decrease caused by the reflector, is 6,580 foot-candles.

With this system it is also possible to study the effect of different regions of the solar spectrum on the plant. Different regions of the spectrum can be obtained with colored glasses and liquid filters. For example, blue (400 mμ to 589 mμ) at 549 foot-candles, orange (538 mμ to 648 mμ) at 1,327 foot-candles, red (600 mμ to 1,360 mμ) at

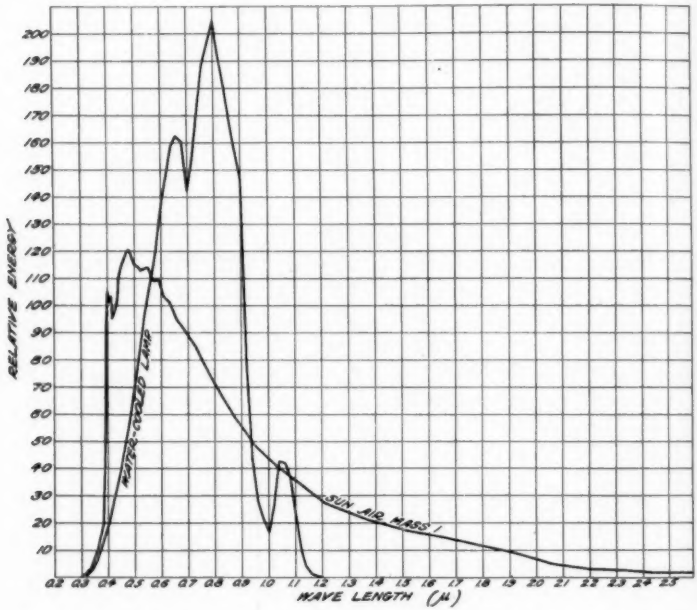

FIGURE 6.—Spectral distribution of the radiation from a 1,000-watt 110-volt water-cooled lamp and from the sun at air mass 1

815 foot-candles, and green (400 mμ to 630 mμ) at 1,609 foot-candles are some of the intensities which have been actually obtained with tray water screens. By the use of larger lamps (2,000–5,000 watt) these values can easily be exceeded and intensities fairly comparable to sunlight obtained. Moreover, by the use of special lamps (mercury, carbon, flame, and neon arcs, etc.) these high intensities under certain conditions can be obtained with greater efficiency.

The light period in the cases is regulated by means of a standard program clock controlling eight light cases and capable of automatically turning the lamps on and off to the minute within an error of one second a day. The assembly consists essentially of a master clock and two secondary or slave clocks. The latter are driven electrically by the master clock, which closes an electric contact each

minute for about two seconds. These secondary clocks are each equipped with two tapes printed in minute intervals and four pronged electric-contact bars. As the tapes rotate intermittently at intervals of one minute, the contact bars are forced down against the tape but can not make electric contact unless a hole has been punched in the tape. If the tape has been perforated at any minute interval the prong passes through the hole, the contact is made, and the lamp is turned on or off through the intervention of relays.

CONTROL OF TEMPERATURE AND HUMIDITY

Temperature and humidity are controlled by means of a hot-blast heating system with air washer and water heater, having a capacity of 4,000 cubic feet of air per minute. It differs in some details from the standard arrangement, since the preheater following the washer has been omitted, and the tempering coil preceding the washer is used in conjunction with a double mixing damper. Control is by means of compressed-air thermostats, which regulate the supply of compressed air to the bellows on the steam and water valves and on the dampers. There is no refrigeration. The only provision made for cooling the entering air is through the use of cold tap water. Provision is also made for recirculating the air in any proportion when required for special conditions of experimentation.

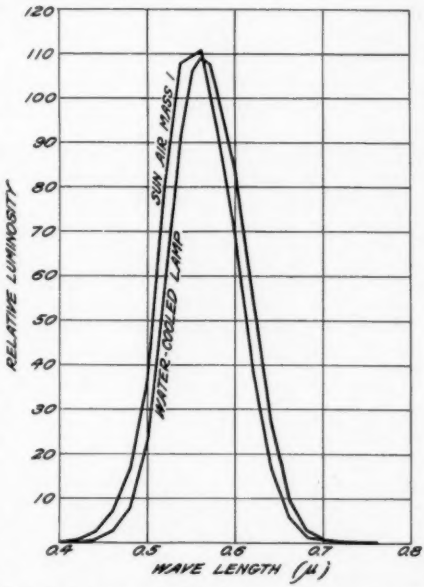

FIGURE 7.—Spectral distribution of the light from a 1,000-watt 110-volt water-cooled lamp and from the sun at air mass 1

The arrangement of the various units is most easily pictured by following the course of the air as it is conditioned. Immediately on entering the system the outdoor air is drawn through a heater (the tempering coil) or by-passed under the heater by means of a thermostat with double or mixing damper, and discharged into the air washer at a constant temperature. Here it is thoroughly sprayed and washed with water and leaves the washer practically saturated with moisture. The temperature of saturation of the leaving air is regulated by two dew-point thermostats at the outlet of the washer. One regulates the volume of steam entering the spray water at the suction side of the recirculating pump. The other regulates the volume of fresh, cold tap water mixed with the warm spray water being recirculated. The air, now containing an approximately fixed

amount of moisture, is again drawn through a heater (the reheater) arrangement similar to that of the tempering coil, where it is raised to the proper temperature by a thermoregulator in the room. Steam is then added under control of the room hygrostat, and the air passes through a blower which forces it into the room containing the cases and over a thermostat controlling the reheater coil and damper.

The control of temperature and relative humidity is very accurate. (Fig. 8.) Air temperature varies only about one-half of 1 degree in the room from which the cases draw their supply of air, and the relative humidity varies only about one-half of 1 per cent.

While it was found possible to attain the above-mentioned accuracy of control of temperature by means of standard compressed-air thermoregulators, the control of humidity by means of standard hygrostats and dew-point thermostats was only to within an error of about ±2 per cent. After considerable experimentation it was found necessary to design a special hygrostat and to use a method of control that is believed to be new.

The hygrostat consists of an air valve actuated by the expansion and contraction of hair. The hair is in three flat bands, each having

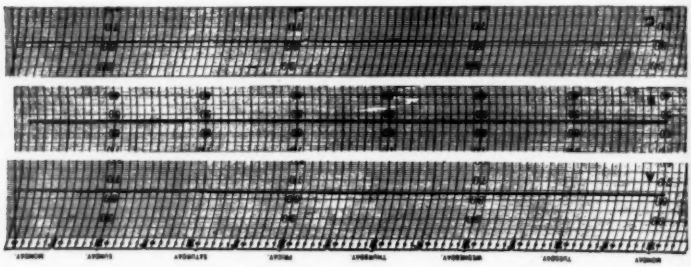

FIGURE 8.—Sample weekly temperature and humidity charts: A, Temperature of the air entering light cases; B, humidity of the air entering light cases; C, temperature of the air leaving light compartments

1,000 hairs 16 inches long. The expansion and contraction of the hair actuate a lever (±6 magnification) which closes and opens an air valve controlling in turn a valve on a steam jet emptying into the blower. The humidity chart (Friez hygrograph) shows a range of only 1 (or ±0.5) per cent in the relative humidity.

In controlling humidity by the new method, no attempt is made to secure accuracy of dew-point control at the washer. The dew point at the washer is held several degrees below that wanted in the control room. The difference is made up by means of the improvised room hygrostat, which controls a small steam jet. A Friez aspiration psychrometer is used to verify temperature and humidity control and to check the recorders from time to time.

The conditioned air after being blown into the room is drawn out through the light cases by means of another blower, which discharges the air outdoors. With this arrangement the temperature differences through the plant compartment are never greater than 1.5° F. (using a 1,000-watt lamp) next to the water screen. Elsewhere in the plant compartment they are never greater than 1°.

The control in the cases is somewhat complicated by the heating effect while the lamp is on. The heat generated by a 1,000-watt

110-volt lamp while burning is 59.6 B. t. u.[5] per minute, or enough to heat 3,275 cubic feet of air 1° F. per minute. The energy output of the lamp under these conditions (lamp with clear bulb and 3-inch water tray interposed) is distributed approximately as follows: Waste, 225 watts; water-screen, 700 watts; and plant compartment, 75 watts. The temperature rise in the water screen is kept down by constant renewal of the water. The computed rise in air temperature due to the 75 watts of radiation that enters the case is

$$\frac{256.1 \text{ B.t.u.}}{0.0182 \times 220 \text{ C.F.M.}^{6} \times 60 \text{ min.}} = 1.07° \text{ F.}$$

This heating effect can be decreased by using a 6-inch water screen without serious loss of light if the distance between lamp and screen is not increased. The writer has found the most practical solution in the use of small adjustable electric heaters, which are on only while the lamps are off.

It was not found practicable to increase the distance between lamp and plant in order to decrease the heating effect of the radiation. Under the usual conditions of short air path both the luminous and dark (infra-red) radiation respond similarly to increase in distance. Readings in the light cases with 1,000-watt lamps, without water screen and with air circulation of 220 cubic feet per minute, gave an air-temperature rise of 12.5° F. at 6 inches from the tip of the lamp. At 17 inches the rise in air temperature was 10.5°. This 2° drop in air-temperature rise was accompanied by a 70 per cent drop in the illumination. A 3-inch layer of water, however, removes about 70 per cent of the total radiation and only 15 per cent of the light. It must be remembered that only about 8 per cent of the energy input, or 13.6 per cent of the total radiation, of a gas-filled lamp is luminous. Filtered through a 1-inch water screen, the radiation is approximately 42 per cent luminous; through a 3-inch screen, 53 per cent luminous.

Figure 8 shows sample weekly records (Friez thermographs and hygrographs) of the temperature and humidity of the air entering the light cases and a temperature record of the air leaving one of the light cases. The variation in temperature and humidity at which the plants are grown is of course ±0.5 of the difference between that of the outgoing and the incoming air.

CONTROL OF AIR VELOCITY

The air entering the room is distributed equally (within an error of ±5 per cent) between the light cases by adjusting the dampers at the top of the cases and measuring with an anemometer the volume of air passing. Constancy in volume of air passed through any case, however, has been much poorer and has varied as much as 20 to 30 per cent on account of variation in the total volume of air conditioned with the present system. This condition will, it is expected, shortly be remedied by reproportioning the inlet ducts so as to give constancy of air volume within an error of ±5 per cent or better. The volume of air passed through each case is about 220 cubic feet per minute, or sufficient to keep the temperature rise due to the entering radiation down to about 1° F. The air velocity over the plants is thus approxi-

[5] British thermal units.

[6] Cubic feet per minute.

mately 80 feet per minute, or 0.9 mile per hour. This is quite low as compared to outdoor conditions at Washington, D. C., if the average wind velocity is taken at 5 miles per hour, or 440 feet per minute. It is nevertheless enough to supply the plants in each case with 7.4 ounces of carbon dioxide per hour, or slightly more than 11 pounds per day. Obviously, the partial pressure of the carbon dioxide can not be materially altered by the plants.

The increase in relative humidity of the air leaving the cases, due to transpiration from the plants, can easily be computed. Assuming a maximum water loss of 2.4 kgm. distributed equally over 24 hours, the increase is well below 1.2 per cent relative humidity at this air velocity and at a temperature of 77° F.

CONTROL OF SOIL MOISTURE

The control of soil moisture in the plant containers has been described in a previous publication (*13*). More recently, however, each rocking funnel has been equipped with a small inexpensive counter that registers the number of times water has been added and in this manner gives a measure of the transpiration. The counters equipped with fork arms are mounted in front of the rocking funnels. The swing of the funnel when water is directed into the box rotates the counter arm sufficiently to add one on the counter, while the return swing leaves the tally unchanged.

The wooden soil containers have been replaced by aluminum containers lined with asphalt applied hot so as to protect the aluminum from the action of the soil. The moisture distributor retains its old form but is placed above the soil in order to increase the uniformity of vertical soil-moisture distribution.

Two corks are used as a seal around the stem of each plant. One is 2½ inches in diameter with a 1½-inch hole bored eccentrically. The other, which is 1½ inches in diameter, is notched at the edge and fits into the hole of the larger cork. By rotation of the two corks, it is possible to make a seal around the stem of a seedling without bending the stem.

DISCUSSION

Of the various environmental conditions light has proved most difficult to control. The radiation of the tungsten lamp is, of course, not identical with that of the sun. To obtain radiation approximating that of the sun an incandescent lamp burning at about double the temperature of the tungsten filament is necessary. The possible future development of lamps burning at higher temperatures appears not at all remote (*10*). Until their appearance, however, the tungsten lamp will probably prove the most satisfactory of all the present light sources.

The only other light source that appears to be practicable as a substitute for sunlight is the white-flame carbon arc. Unfortunately in its present state of development it is far from satisfactory for such use, except possibly in experiments of very short duration. While the radiation of this lamp approximates sunlight more closely than that of any other source of artificial light (*4*), its use is objectionable because of the short life of the carbons, the flickering of the light, and the continuous deposition of ash on the inclosing globe. If an attempt is made to dispense with the globe, the carbons last only a few hours.

Other sources of artificial light are either of too weak an intensity or have line or band spectra too widely different from that of sunlight to assure comparable results.

It is hoped that the lighting will be improved in the near future in another particular, namely, the uniformity of distribution. Under present conditions uniformity within an error of ±6 per cent can be attained only at a distance of not less than about 1 foot from the lamp. The wastage of light is felt to be too great under these conditions, however, and uniformity within an error of ±10 per cent at a distance of not over 3 inches should be feasible, if proper incentive is given the manufacturer to develop the special type of reflector required for work of this character.

There are several additional points concerning the illumination that might prove of interest. Of the 1,000-watt energy input of a tungsten lamp, 80 watts emerges as light. At 100 per cent over-all efficiency, the illumination in cases 20 inches square would be about 7,600 foot-candles, and the temperature rise of the circulating air (220 cubic feet per minute) slightly more than 1° F. According to the lamp manufacturers, the color temperature of the lamp may drop 100° K. before the lamp burns out, while total lumens may drop 15 per cent. Maximum manufacturing tolerance in initial total lumens is ±12.35 per cent with new lamps, although 80 per cent of the lamps are within half these limits. The use of walls with high light reflectivity, as, for example, polished silver plate, or special paints, should result in increased intensity and uniformity of illumination as compared with the white enamel which has been used. Any attempt made to conserve and use the ultra-violet radiation should include the use of Corex glass or quartz for transmission, and chromium plate, polished or oxidized aluminum, or Monel metal for reflection.

Despite the emphasis placed on difficulties with the present lighting system, the conditions of growth in the light cases are not so different from those outdoors that comparable results can not be obtained. Agreement in the results of different experiments in the light cases and between these and results obtained outdoors is generally well within an error of 10 per cent, and probably is susceptible of further improvement.

SUMMARY

An installation suitable for accurately determining the response of plants to changes in their environment has been briefly described. It comprises eight light cases for growing plants; a modified hot-blast heating system, with air washer controlled pneumatically, for regulating the temperature, humidity, and air velocity; an automatic watering system to maintain constant soil moisture and record transpiration; and a program instrument for turning the lamps on and off automatically. The lighting units (water-cooled lamps) consist of tungsten lamps in special bulbs for burning when immersed in water. It provides for control of the day length to within a total error of ±10 seconds per month, of light intensity to within a total error of less than ±10 per cent according to the duration of lamp burn, of light quality to within a color-temperature variation of ±100° K., of temperature to within an error of ±0.5° F., of humidity to within an error of ±0.5 per cent, of air velocity to within an error of ±5 per cent, and of soil moisture to within an error of ±1 per cent.

Each light case has a cross section of about 2¾ square feet and will accommodate plants 4 feet in height.

Included in this description is a method for increased accuracy of pneumatic humidity control and an improved lighting unit which is also suitable for conducting experiments with colored light.

Agreement in the results of different experiments with this equipment and between these and results obtained outdoors is generally well within an error of 10 per cent, and probably is susceptible of further improvement.

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INHERITANCE OF RESISTANCE IN OATS TO USTILAGO LEVIS[1]

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INTRODUCTION

The control of oat smuts through the breeding of resistant strains is of wide interest because of the economic importance of these diseases. This paper presents the results of studies on the inheritance of resistance to infection by *Ustilago levis* (Kell and Sw.) Magn. Genetic data were obtained on six crosses, and some rather fragmentary data on three others. Approximately 140,000 plants were observed. Data were recorded on (1) the percentage of individuals resistant to *U. levis* in F_2 and later generations, (2) the relation of infection in F_3 lines to infection in selections from them in later generations, and (3) the relation between certain morphological characters and resistance to smut infection in progeny plants. The study was conducted during 1925, 1926, and 1927, and data collected at five widely separated points are presented.

REVIEW OF LITERATURE

Wakabayashi (*15*)[2] published the first report in this country on the inheritance of the resistance of oats to infection by smut. He crossed Red Rustproof (resistant) with Black Tartarian (susceptible). The indicated dominance of resistance was attributed to three independent dominant factors. His results indicated that correlation existed between lemma color and resistance to smut infection in the cross studied.

Barney (*1*) concluded that resistant varieties contained either one, two, or three factors for resistance to smut. Gaines (*3*) studied crosses between Red Rustproof and Black Tartarian, Abundance, Large Hull-less, and Chinese Hull-less. He reported that Red Rustproof has three factors for resistance. Reed and Stanton (*13*), studying the cross Fulghum × Swedish Select, observed no correlation between the morphological characters studied and resistance to smut. Gaines (*4*) concluded that the smut-resistant Markton probably contains three factors for smut resistance. In crosses between Black Mesdag, resistant to both loose and covered smuts, and Hull-less, susceptible to both, Reed (*9*) observed that resistance was dominant to susceptibility. Segregation in the F_2 indicated a single-factor difference between the parents. In later experiments Reed (*11*) observed similar results from crosses of Hull-less × Black Mesdag, and Silvermine × Black Mesdag. He studied the inheritance of resistance to smut infection in several other crosses, and

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[2] Reference is made by number (italic) to Literature Cited, p. 1099.

states that "In all crosses involving varieties differing in their behavior to smut, resistance was dominant and susceptibility recessive, and segregation in the F_2 appeared to occur on the basis of a single-factor difference."

Hays, Griffee, Stevenson, and Lunden (*6*) studied resistance in crosses of Black Mesdag with homozygous strains from the cross Minota × White Russian. They state that "immunity to smut in oats is dominant to susceptibility." No correlation was found between glume color, awn development, hairs on the rachilla segment, and smut resistance. They found it impossible to state the exact genetic constitution of their material as to smut resistance.

Garber, Giddings, and Hoover (*5*) found in the cross Gopher × Black Mesdag that no relation existed between smut susceptibility and earliness. They suggest a possible linkage between black seed color and a supplementary factor for transgressive segregation of smut susceptibility, but little if any linkage between leaf width and resistance to smut. They conclude that Gopher and Black Mesdag differ in their reaction to smut infection by a single main factor, and in addition by at least one modifying factor, presumably present in Black Mesdag, which resulted in transgressive segregation for susceptibility.

MATERIALS AND METHODS

Markton, so far as known, is immune under field conditions to both the loose and covered smut strains generally found in the United States. Data were obtained on crosses of this variety with the susceptible varieties Early Champion, Ligowa, Scottish Chief, Swedish Select, Iogren, and Aurora. Some data also were obtained on crosses of Markton with Victory, Idamine, and Silvermine. Several strains of the Iogren and Silvermine varieties were tested by Reed, Griffiths, and Briggs (*12*). Iogren is a selection from Green Russian, and Idamine a selection from a commercial strain of Silvermine known as Funk. Morphological descriptions of all these varieties are available.

In studies of the relative susceptibility of oats to *Ustilago avenae* and *U. levis*, respectively, Reed et al. (*12*) classified the above varieties, or varieties closely related to them, as follows:

Highly susceptible to both smuts: Early Champion, Silvermine.
Moderately susceptible to both smuts: Green Russian, Ligowa, Swedish Select, Silvermine, Victory.
Less resistant to *U. avenae* than to *U. levis:* Aurora, Green Russian, Scottish Chief.

All the crosses were made at the Aberdeen substation, Aberdeen, Idaho. The inoculum used in 1925 and 1926 was collected almost entirely at Aberdeen. It was identified as *Ustilago levis* with a very slight admixture of *U. avenae*. Later, field cultures proved this identification correct. The smut inoculum used in 1927 at all stations and on all crosses except those involving Iogren was isolated and cultured in the greenhouse at the Arlington Experiment Farm, Rosslyn, Va., during the winter of 1926–27. The Iogren crosses grown in 1927 were inoculated with smut furnished by Dr. George M. Reed, curator, Brooklyn Botanic Garden, Brooklyn, N. Y.

The inoculum was prepared by grinding the smutted panicles. Inoculations were made by thoroughly blackening the oat seed with smut spores and shaking the seed and spores in envelopes.

It was shown by Jensen (*7*) as early as 1887, subsequently by others, and more recently by the present writers (*2, 14*), that removing the lemma and palea from the oat kernel prior to inoculation with *Ustilago levis* increases the percentage of smut-infected plants. Except in the case of occasional undersized F_2 plants, 100 kernels from each F_2 plant were sown in growing the F_3 of three of the six crosses studied. Two were sown at the rate of 33 and one at the rate of 50 kernels from each F_2 plant. In growing the F_4 and F_5 in each of two crosses, 80 kernels of each plant chosen were sown, and in each of the remaining crosses usually 40 kernels were sown. In one cross all seed of a single panicle was sown. The glumes were removed from all kernels prior to inoculation in cases where less than 100 were sown per family. When 100 kernels were sown the glumes were removed from half the number.

The F_1 plants of all hybrids were grown in the greenhouse at the Arlington Experiment Farm. The F_2 generations of all but two crosses were grown at the Aberdeen substation in 1924 or 1925. The F_2 generation of the others was grown at the Sherman County branch station, Moro, Oreg., in 1924. Data on smut infection in the F_2 were obtained only on the crosses Markton × Iogren and Markton × Silvermine. Studies were made on subsequent generations of the different crosses at Aberdeen, Idaho; Ames, Iowa; Moro, Oreg.; Dickinson, N. Dak.; and Moccasin, Mont. At Aberdeen the crop was grown under irrigation. The climate at Ames is humid and moisture usually is ample. At the other stations subhumid or dry-land conditions prevail. Climatic conditions were comparatively normal at all stations while the experiments were in progress.

In this study any plant that showed any degree of smut was considered infected.

INHERITANCE DATA

Data on the susceptibility to smut infection of the parent varieties grown as checks are given in Table 1. Data for the inheritance of resistance to smut infection in the different crosses are given in Table 2. Data for distribution of F_3 lines according to degree of infection are given in Table 3. The data for each cross are discussed separately.

TABLE 1.—*Percentage of infection by Ustilago levis in susceptible parent varieties grown adjacent to the six crosses studied genetically*

[Markton produced no smutted plants at any station in any season]

Susceptible parent variety	Station where grown	Percentage of infection			
		1925	1926	1927	Maximum
Early Champion	Moro, Oreg.	100.0	99.0	.....	100.0
Ligowa	...do	86.6	78.9	.....	86.6
Scottish Chief	...do	24.6	20.6	.....	24.6
Swedish Select [a]	Dickinson, N. Dak.	80.6	74.2	20.0	80.6
Iogren	Aberdeen, Idaho	93.0	.....	[b] 96.6	96.6
Do	Ames, Iowa	.....	39.0	.....	.....
Do	Moccasin, Mont.	.....	.....	[b] 78.0	.....
Aurora	Aberdeen, Idaho	55.0	19.2	.....	55.0
Do	Ames, Iowa	.....	12.8	.....	.....

[a] Swedish Select smutted 63.0 per cent at Moro, Oreg., in 1926.

[b] Inoculum used was obtained from the Brooklyn Botanic Garden. In all other tests the smut strain originally obtained at Aberdeen, Idaho, was used as inoculum.

TABLE 2.—*Number and percentage of progeny lines from F_2 plants of oats infected by Ustilago levis in crosses between the smut-resistant Markton and six susceptible varieties grown in tests at five experiment stations in 1925, 1926, and 1927*

Variety crossed with Markton	Station where grown	Year grown	Generation tested	Number of progeny lines—			Summary of comparable data for cross		
				Smut free	Infected	Total	Number of lines grown	Lines infected	
								Number	Per cent
Early Champion	Moro, Oreg	1925	F_3	38	101	139			
Do	do	1926	F_4	35	3	38			
Summary							139	104	74.8
Ligowa	Moro, Oreg	1925	F_3	21	48	69			
Do	do	1926	F_4	20	1	21			
Summary							69	49	71.0
Scottish Chief	Moro, Oreg	1925	F_3	47	48	95			
Do	do	1926	F_4	44	3	47			
Summary							95	51	53.7
Swedish Select	Dickinson, N. Dak	1925	F_3	57	78	135			
Do	do	1926	F_4	46	11	57			
Do	do	1927	F_5	44	2	46			
Do	do	1927	F_3 [a]	80	14	94			
Summary							135	93	68.9
Iogren	Aberdeen, Idaho	1925	F_7	171	12	183			
Do	Ames, Iowa	1926	F_3	136	35	171			
Do	Aberdeen, Idaho [b]	1927	F_3 [a]	42	35	77			
Do	Moccasin, Mont. [b]	1927	F_3 [a]	30	40	70			
Summary							183	96	52.5
Aurora	Aberdeen, Idaho	1925	F_3	74	72	146			
Do	do [c]	1926	F_4	62	2	64			
Do	Ames, Iowa [c]	1926	F_4	74	0	74			
Summary							146	74	50.7

[a] Recheck of previously tested F_3 material using remnant seed.
[b] Inoculum used was from a different source from that used in other tests.
[c] Duplicate seedings so far as seed was available.

TABLE 3.—*Distribution of F_3 progeny lines of crosses of Markton oats with six varieties based on percentage of plants infected by Ustilago levis*

[Markton sown for comparison was free from smut in all tests]

Variety crossed with Markton	Number of F_3 lines in infection percentage indicated (class centers)												Total F_3 lines	F_3 lines infected	Mean of infection in F_2 lines	Infection in susceptible parent
	0	5	15	25	35	45	55	65	75	85	95	100				
													Number	*Per cent*	*Per cent*	*Per cent*
Early Champion	38	22	22	13	7	15	5	4	3	5	1	4	139	72.7	24.2	100.0
Ligowa	21	7	17	6	9	4	3			2			69	69.6	18.4	86.6
Scottish Chief	47	21	15	6	4	1				1			95	50.5	7.9	24.6
Swedish Select [a]	57	50	15	6	4	3							135	57.8	6.7	80.6
Do	44	25	8	4	2	1	2	1					87	49.4	7.3	63.0
Iogren [b]	136	23	7	2		2						13	183	25.7	9.1	39.0
Do	42	14	6	7	5			1	1		1		77	45.5	9.7	96.6
Do	30	14	11	9	5	1							70	57.1	9.7	78.0
Aurora	74	51	15	5	1								146	49.3	4.4	55.0

[a] The first group of these strains was grown at Dickinson, N. Dak., in 1925, the second group at Moro, Oreg., in 1926.
[b] The first group of these F_3 strains was grown at Ames, Iowa, in 1926; the second and third groups include data obtained in rechecking experiments by sowing remnant F_2 seed at Aberdeen, Idaho, and Moccasin, Mont., in 1927. In the first group of this cross are included as 100 per cent infected 12 infected F_2 plants grown at Aberdeen, Idaho, in 1925.

MARKTON × EARLY CHAMPION

The cross Markton × Early Champion was studied at the Sherman County branch station in 1925 and 1926. A total of 139 F_3 families was grown, of which 101 showed infection. When the 38 smut-free

F_3 populations were further tested in the F_4, three additional strains produced smut. Of the original 139 F_2 plants, 104 were shown by their breeding behavior to be smut susceptible or heterozygous, and 35 to be smut free. These data, though limited, show that susceptible and segregating strains predominated, and might indicate a single-factor difference for resistance.

MARKTON × LIGOWA

Of 69 F_3 populations of the cross Markton × Ligowa, grown at Moro, Oreg., in 1925, 48 produced smut and 21 were smut free. In the F_4 generation one of the 21 strains not infected in F_3 was smutted. Of the 69 F_2 plants 49 were shown by their breeding behavior to be smut susceptible or heterozygous. The susceptible and segregating strains predominated, and a single-factor difference for resistance between the parents is indicated.

MARKTON × SCOTTISH CHIEF

Of 95 F_3 populations of the cross Markton × Scottish Chief grown at Moro, Oreg., in 1925, 48 produced smut and 47 were smut free. In the F_4 3 of the 47 families smut free in F_3 contained smut-susceptible plants. Of the original 95 F_2 plants 51 were shown to be susceptible or heterozygous and 44 remained smut free.

These results might indicate a 9:7 genetic ratio involving two factors for resistance in this cross. As shown in Table 1, the Scottish Chief parent seems to possess more resistance to smut infection than does either Early Champion or Ligowa, indicating that these varieties may differ from the Scottish Chief variety in their genetic constitution.

MARKTON × SWEDISH SELECT

In 1925, 135 F_3 lines of the cross Markton × Swedish Select were grown at the Dickinson substation, Dickinson, N. Dak. Smutted plants were produced in 78 families and 57 families were smut free. Of the 57 smut-free families in F_3, 11 produced smutted plants in the F_4. When further tested in the F_5 two additional lines produced smut. A recheck of the F_3 made by sowing remnant F_2 seed showed two lines to be susceptible which had not contained smutted individuals in the previous tests.

Summarizing the results of the cross, 93 of the 135 F_2 plants were shown to be susceptible or heterozygous, and 42 produced progeny free from smut. The data might indicate a ratio of 3 susceptible and heterozygous to 1 resistant, but if so, the deviation from the expected is wide. However, more than twice as many lines were infected as were smut free.

In addition to the above study, 87 F_2 plants of this cross not grown at Dickinson in 1925 were studied in the F_3 at Moro, Oreg., in 1926. Of these, 44 lines were free from smut and 43 were infected. The smut-free lines of this group were not tested further. These data are not included in Table 2.

The data on this cross from the two stations if added together would give little definite genetic information. There is reason to believe that the data from the two stations are not comparable. Owing to a difference in the virulence of the inoculum, the age of the seed, or a climatic condition, the infection at Moro in 1926 was less than at Dickinson in either year. Even the susceptible Swedish

Select parent showed only 63 per cent infection at Moro, while at Dickinson infection percentages were 80.6 and 74.2 in 1925 and 1926, respectively. Considering all the data, however, it is evident that susceptible and heterozygous strains were more numerous than resistant ones.

IOGREN × MARKTON

The F_2 of the cross Iogren × Markton was grown from smutted seed at Aberdeen, Idaho, in 1925. Of the 183 F_2 plants, 12 were infected with smut.

An F_3 generation from the smut-free F_2 plants was grown at Ames, Iowa, in 1926. Of the 171 F_3 lines, 35 produced smut.

In a recheck of the F_3, in which remnant seed of the F_2 plants was used, 70 F_3 families were grown at Moccasin, Mont., and 77 F_3 families at Aberdeen in 1927. Inoculum used in 1927 was supplied by George M. Reed, of the Brooklyn Botanic Garden. Of the 70 lines grown at Moccasin 40 produced smut. Of these 40 infected lines 12 had been infected at Ames in 1926. Two lines producing smut at Ames were not grown at Moccasin, and one line infected at Ames was smut free at Moccasin. Of the 77 lines grown at Aberdeen 35 produced smutted plants. Two lines infected at Ames were smut free at Aberdeen, and 14 lines were smutted in both tests. Three lines producing smut at Ames were not grown at Aberdeen, because of lack of seed.

Of 183 F_2 plants 12 were infected in the F_2; including all F_3 data, an additional 84, or a total of 96, proved susceptible or heterozygous. The Iogren parent smutted 96.6 per cent at Aberdeen in 1927. Evidently the study should have been continued in order to obtain reliable genetic information.

AURORA × MARKTON

Of the 146 F_3 populations of the cross Aurora × Markton grown at Aberdeen in 1925, 72 produced smut and 74 were smut free. An F_4 generation of the 74 smut-free lines was grown at Ames in 1926, and a comparable F_4 test of 64 of the same lines at Aberdeen the same year. Conditions were unfavorable at Ames, and none of the families produced smut. Two of the families grown at Aberdeen produced smut.

Of the 146 strains on which data were obtained, 74 were susceptible or heterozygous and 72 did not become infected in two tests. Much of the material of this cross was grown at Ames, but for some unknown reason poor stands and poor infection make the data obtained at Ames of doubtful significance. However, the data from both stations show that susceptible and segregating strains were slightly more numerous than noninfected strains. Data obtained under conditions more favorable for infection might show results conforming essentially to those of the other crosses. On the basis of lower infection percentages there is some reason to believe that Aurora itself differs genetically from Early Champion and Ligowa in resistance to smut infection.

ADDITIONAL CROSSES

Some data were obtained on the inheritance of resistance to smut in three additional crosses. The number of F_2 plants from which populations could be produced was too small to give results of much genetic significance, and the data obtained are not presented in tabular form.

Of 39 F_3 families of the cross Markton × Victory grown at Aberdeen in 1925, 19 produced some smut and 20 produced only smut-free plants. Seed from random-selected plants of 14 of the 20 smut-free families and of 1 smut-susceptible line was divided, half the seed of each plant being sown at Aberdeen and half at Ames. No smut infection occurred in the material grown at Ames, but 2 of 14 lines produced smut at Aberdeen. The line susceptible in F_3 also produced smut in F_4. When tested further in F_5, none of the lines that were smut free in previous generations showed susceptibility. Of the 39 lines of this cross, 21 were smut susceptible or heterozygous. Of the 18 smut-free lines, 6 were tested but once. Freedom from smut in some of these 6 may have been merely "escapes." Too few lines were available to give data of significant genetic value. Susceptible and heterozygous strains, however, did predominate. The Victory parent tested in comparison with the hybrids smutted 93.0, 76.8, and 85.4 per cent at Aberdeen in 1925, 1926, and 1927, respectively, and 40.3 per cent at Ames in 1926.

Of 27 F_3 lines of a Markton × Idamine cross, 5 produced smut. Of the 22 lines free from smut in F_3, 10 were tested further, half the seed of each chosen progeny plant being sown at Aberdeen and half at Ames. Of the 10 lines, 4 produced smut at Aberdeen only, 1 produced smut at both Aberdeen and Ames, and 5 were smut free at both stations. A further test of the 5 lines that were smut free in F_4 showed no smut in these previously smut-free lines.

The genetic value of the above data is doubtful. They differ from those previously presented in this paper in the predominance of smut-free strains, but this difference probably is more apparent than real. While 17 out of 27 lines were free from smut during the period of the experiments, only 10 of the 22 lines not infected in F_3 were tested further. Of these 10 lines 5 became infected in F_4. As these 10 strains were chosen at random, it seems reasonable to assume that had all 22 lines been fully tested the number of infected lines would have exceeded the 10 actually shown by the data.

The Idamine parent smutted 76.6, 61.2, and 64.5 per cent at Aberdeen in 1925, 1926, and 1927, respectively, and 61.8 per cent at Ames in 1926.

An F_2 generation of the cross Silvermine × Markton was grown from inoculated seed at Aberdeen in 1925. Of 56 plants 3 were infected and 53 were smut free. An F_3 generation of the 53 smut-free plants was grown at Ames in 1926. Six of the 53 F_3 families produced smut. In a second F_3 test 45 lines were grown from remnant F_2 seed at Aberdeen in 1927. In this test 17 families produced smut. One line not grown at Aberdeen in 1927 became infected at Ames in 1926, and 5 lines that smutted at Ames in 1926 again smutted at Aberdeen in 1927. By combining F_2 and F_3 data, 21 smutted to 35 smut-free segregates were observed in this cross. This result is similar to that obtained for Markton × Idamine, the latter a close relative to Silvermine, and might seem to substantiate a genetic condition in Idamine and Silvermine differing from that in the other varieties studied. It must be borne in mind, however, that the present cross was not studied in F_4 for a further checking of susceptibility. The doubtful reliability of the data for the cross Markton × Idamine has already been pointed out. Until better evidence is forthcoming,

therefore, there is no proof of any distinct genetic difference in the smut resistance of these two varieties and the others previously considered.

The Silvermine parent smutted 35.7 and 76.7 per cent in 1925 and 1927, respectively, at Aberdeen, and 47.7 per cent at Ames in 1926.

CORRELATION OF RESISTANCE IN F_3 AND F_4

Several investigators have classified F_2 plants genetically on the basis of the percentage of infection in the F_3 and later progenies; that is, it has been assumed that the F_2 parent plant of an F_3 line in which 30 per cent of the plants became infected differs in factorial constitution from the F_2 parent plant of an F_3 line in which only 10 per cent of the plants were infected.

The smut reaction of F_4 populations of families from each of four crosses was studied statistically by the writers in an attempt to determine the relationship in reaction between different generations of the same cross. The hulls were removed from all seed prior to inoculation. Not less than 40 and in most cases 50 or more kernels were sown from each F_3 plant. The inoculum and methods were the same as those discussed in the foregoing pages. Data presented in Table 4 are discussed separately for individual crosses. To make the study as complete as possible, all data from the F_4 progeny rows grown from smut-free F_3 populations are included. As a result, the classes of progeny grown that had no infection (0) in the F_3 are very large as compared with the others.

TABLE 4.—*Distribution of progeny of different F_3 lines of oats according to percentages of infection in F_4 progeny of four crosses of Markton (resistant) with the smut-susceptible varieties named*

Variety crossed with Markton and F_3 plant No.	Infection in F_3 plant	Number of F_4 progeny in infection percentage class indicated (class centers)												F_4 lines grown	Mean infection	Correlation for cross; r=
		0	5	15	25	35	45	55	65	75	85	95	100			
Early Champion:	*Per cent*													*Number*	*Per cent*	
1071a–x	0	111	3											114	0.1	
1071a–1–10	1.3	11												11	0	
1071a–2–19	6.3	15												15	0	
1071a–3–42	15.4	3	2	1	3	2								11	15.5	
1071a–2–5	28.4	9		1										10	1.5	
1071a–3–25	36.4	7	1											8	0.6	
1071a–2–14	44.7	7		1		3								11	10.9	
1071a–2–18	56.1	4			1	1	2				1	1		10	33.0	
1071a–3–15	66.6	3	2	2	1									8	8.1	
1071a–2–54	76.3	1		1										2	7.5	
1071a–2–29	85.2	1		1	1									3	13.3	
1071a–2–44	92.2					1							1	2	67.5	
1071a–2–23	92.9												2	2	100.0	+0.574±0.031
Swedish Select:																
1069a–x	0	211	4	6	5	1	1							228	1.4	
1069a–5–4	2.4	36	2											38	.3	
1069a–6–10	9.4	18	2	4	4	4	5	4	5	2	2		2	52	30.8	
1069a–6–43	18.9	26	3	4	1	2	3	2		2				43	13.1	
1069a–4–20	30.2	14	1	6	7		7		4	2			1	44	28.8	+.458±.026
Aurora:																
1072a–x	0	220	1	1										222	.1	
1072a–2–12	8.6	55	2											57	1.2	
1072a–2–23	9.5	67	10	4	2									83	1.9	
1072a–2–13	16.7	38	24	18	1		1							82	5.6	
1072a–3–47	23.4	29	22	24	8									83	8.1	+.507±.022
Scottish Chief:																
1065a–x	0	138	3											141	.1	
1065a–2–39	1.6	39												39	0	
1065a–3–9	15.9	25	2	1	1		1							30	3.2	
1065a–2–19	34.3	9	8	3	6	3	2	2	3	1	1			38	23.6	
1065a–2–1	82.5					1	1	2	7	7	6	11	5	40	80.6	+.913±.007

MARKTON × EARLY CHAMPION

The study of the cross Markton × Early Champion was made at Moro in 1926. The infection percentages of 12 parent F_3 strains chosen for study varied from very low to very high by approximately 5 to 10 per cent gradations. In addition, three plants were selected from each of the 38 smut-free lines for testing in F_4. Infection in the F_4 progeny showed significant correlation with infection in the F_3, $r = +0.574 \pm 0.031$. The F_4 lines naturally showed some tendency toward less infection than the F_3 lines, since F_4 populations could be grown only from smut-free or partially smutted F_3 plants.

MARKTON × SWEDISH SELECT

A study of the cross Markton × Swedish Select was made at Dickinson in 1926. The four F_3 lines chosen for study in the F_4 varied in the percentage of smut infection present. In addition to the smutted plants, three plants were selected for study from each of the 57 smut-free F_3 lines. Correlation between F_3 and F_4 infection in this cross was $r = +0.458 \pm 0.026$. It is interesting to note that one of the most heavily infected F_4 populations was from an F_3 line having a comparatively light infection percentage. The total infection range, however, was only 28 per cent. Transgressive segregation for susceptibility to smut infection occurred in progeny of this cross. Higher percentages of infection were observed in some of the hybrid lines than in the susceptible Swedish Select parent.

AURORA × MARKTON

Data on the cross Aurora × Markton were obtained at Aberdeen in 1926. The four F_3 lines chosen for study in the F_4 varied in smut infection percentages. Also a total of 222 lines, or three lines from each of 74 F_3 lines, was tested. The range in infection percentages between the various lines was only 12.8 per cent. Significant correlation was found between F_3 and F_4 infections, $r = +0.507 \pm 0.022$.

MARKTON × SCOTTISH CHIEF

The cross Markton × Scottish Chief was studied at Moro in 1926. All the plants from four infected lines and three plants each from 47 smut-free lines were tested in F_4. Duplicate seedings of each F_3 line of this cross had been grown; one inoculated with smut, the other not inoculated. Seed used for growing the F_4 generation was taken from the material not inoculated in F_3. As a result, susceptible individuals had not been eliminated in the F_3 and there was a higher correlation between F_3 and F_4 infections in this cross than in any of the others studied. Correlation was relatively high, $r = +0.913 \pm 0.022$. It is of interest to observe in connection with these studies that transgressive segregation for susceptibility to smut infection, as in the Markton × Swedish Select cross, was also indicated in the progeny of this cross. Some progeny lines produced higher percentages of smut than were observed in the susceptible Scottish Chief parent. This observation was made by Garber, Giddings, and Hoover (*5*) in the cross Gopher × Black Mesdag.

RELATION BETWEEN MORPHOLOGICAL CHARACTERS AND RESISTANCE TO SMUT INFECTION

A knowledge that linkage exists between a morphological character and either disease resistance or susceptibility is of definite service to the plant breeder. Linkage of this type in oats was indicated by Wakabayashi (*15*), although others have observed little or no correlation between morphological characters and smut reaction in this crop. Data are here presented on the relationship between the characters susceptibility to smut infection and panicle length, kernel length, kernel width, awns, prominence of nerves, and lemma color. The differences of the means are computed for the characters susceptibility to smut infection and panicle and kernel length. The value of Q has been computed for the characters susceptibility to smut infection and kernel width, awns, prominence of nerves, and lemma color. The association coefficients were computed by the method described by Yule (*16*).

PANICLE LENGTH

The relation between panicle length of the F_2 and resistance to smut infection in F_3 and later generations was studied in the crosses Markton × Swedish Select and Aurora × Markton. Markton, the resistant parent of these crosses, has a much longer panicle than either of the other varieties. The distribution for the two crosses is presented in Table 5. The data indicate no relationship between panicle length in the F_2 and smut infection in the F_3 progeny. Differences between the mean of infected and smut-free plants in the two crosses were 0.16 ± 0.09 and 0.30 ± 0.13, respectively.

TABLE 5.—*Mean panicle lengths of F_2 plants shown to be susceptible and of those shown to be resistant to smut infection by later generation progeny populations*

Cross and smut reaction of progeny	Number of progeny from parents having indicated panicle length (inches)									
	4. 1–5	5. 1–6	6. 1–7	7. 1–8	8. 1–9	9. 1–10	10. 1–11	11. 1–12	Total	Mean
Markton×Swedish Select:										
Infected		1	2	10	43	67	22	7	152	9. 26±0. 06
Smut free		0	0	6	27	26	11	0	70	9. 10± . 07
Difference										. 16± . 09
Aurora×Markton:										
Infected	1	6	9	23	17	16	0	0	72	7. 85± . 10
Smut free	0	1	10	22	27	10	3	1	74	8. 15± . 09
Difference										. 30± . 13

KERNEL LENGTH

The crosses studied in the experiment on kernel length were the same as those in the experiment on panicle length. The resistant Markton has unusually long kernels, while those of the other varieties are very short. In determining kernel length, five primary kernels taken at random from each plant were measured and averaged. The data are given in Table 6. There was no apparent relation between kernel length and resistance or susceptibility to smut in these two crosses. Differences between the mean of infected and smut-free plants of the two crosses were 0.03 ± 0.08 and 0.06 ± 0.12, respectively.

TABLE 6.—*Mean kernel lengths of F_2 plants shown to be susceptible and of those shown to be resistant to smut infection by later generation progeny populations*

Cross and smut reaction of progeny	Number of progeny from parents having indicated kernel length (mm.)								
	14. 1–15	15. 1–16	16. 1–17	17. 1–18	18. 1–19	19. 1–20	20. 1–21	Total	Mean
Markton×Swedish Select:									
Infected	.....	6	38	80	26	2	.....	152	17.37 ±0.04
Smut free	.....	2	24	28	15	1	.....	70	17.34± .07
Difference	.....	.....	.....	.....	.....	.....	.....	.....	.03± .08
Aurora×Markton:									
Infected	1	5	22	25	15	2	2	72	17.36± .09
Smut free	1	6	16	32	13	6	0	74	17.42± .08
Difference	.....	.....	.....	.....	.....	.....	.....	.....	.06± .12

KERNEL WIDTH

The same two crosses also were studied for relation between kernel width and resistance to smut. Kernel width was determined by measuring in millimeters five primary kernels taken at random and averaging the results. All kernels 3 mm. or more in width were grouped as wide, and those less than 3 mm. as narrow. The data are presented in Table 7. Little or no relation is indicated in the crosses studied. In one cross $Q = +0.037 \pm 0.045$, and in the other $Q = -0.357 \pm 0.049$.

TABLE 7.—*Association between kernel width in F_2 plants and susceptibility to smut infection of progeny of these plants in later generations*

Cross and smut reaction of progeny	Number of progeny of parents having indicated kernel widths			Q
	Wide (3 mm. or over)	Narrow (less than 3 mm.)	Total	
Markton×Swedish Select:				
Infected	81	71	152	.....
Smut free	36	34	70	+0.037±0.045
Aurora×Markton:				
Infected	59	13	72	.....
Smut free	67	7	74	−.357± .049

AWNS

The smut-resistant parent Markton is awned. The susceptible parent Aurora is almost completely awnless. The coefficient of association between awns and smut infection for the cross Aurora×Markton was $Q = -0.052 \pm 0.056$.

PROMINENCE OF NERVES

The nerves, the fibrovascular bundles running longitudinally through the oat lemma, are much more prominent and more easily observed in some varieties of oats than in others. In the resistant Markton they are readily identified, while in the susceptible Swedish Select, Scottish Chief, and Aurora they blend into the adjacent tissue and are somewhat obscured. A study of relationship of lemma

nerves to smut infection in crosses of Markton with these three varieties was made. The coefficients of association for the three crosses, $Q = -0.214 \pm 0.043$, $+0.202 \pm 0.066$, and $+0.083 \pm 0.055$, respectively, indicate that prominence of nerves has no relation to resistance to smut.

LEMMA COLOR

The lemmas of the resistant Markton are yellow; those of the susceptible Swedish Select and Scottish Chief are white. The relationship of lemma color to smut infection in the crosses Markton × Swedish Select and Markton × Scottish Chief was studied. The coefficient of association for the first cross, $Q = +0.094 \pm 0.045$, would indicate no relation between these characters. The coefficient for the second cross, $Q = +0.632 \pm 0.042$, would indicate a high degree of correlation.

DISCUSSION

The results presented differ from those of previous studies, owing possibly in part to the use of different technic. The removal of hulls prior to inoculation resulted in unusually high infection percentages both in susceptible parents and in hybrid populations. This procedure has not been followed before in genetic studies, nor have the varieties employed in the experiments been used previously in reported studies of this nature. Except for a statement by Gaines (*4*), nothing relative to the genetic nature of the smut immunity of Markton appears to have been published. Gaines states:

> Data on F_3 families of Markton × Large Hull-less and Markton × Banner, grown at Pullman, Washington, in 1926, and as yet not completely analyzed, show the immunity of Markton to be dominant but controlled by multiple factors—probably three.

Reed (*8, 10*) has demonstrated the existence of several physiologic forms of *Ustilago levis*. Differences in the reaction of host varieties to various physiologic forms might give different genetic results in the same oat cross from inoculum of different forms.

Seasonal and place variations in smut infection also may modify apparent segregations. It seems evident that until a more certain technic is evolved care should be exercised in drawing conclusions relative to the factors involved in the inheritance in oats of resistance to infection by smut in field experiments. Moreover, conclusions should be specifically limited to the smut strains used, and some consideration should be given to climatic conditions and other factors affecting infection.

The data herein given show that, with the present technic of artificial inoculation for smut infection in oats, genetic interpretations based on the percentage of smut-infected individuals in F_3 may not be accurate. As pointed out, the effect of seasonal fluctuations in infection certainly can not be ignored. In all but one cross in the experiments reported herein the growing of F_4 populations from seed produced by the inoculated F_3 probably reduced true association. Completely susceptible F_3 plants were destroyed by smut, and the F_4 progenies were grown, therefore, only from wholly or partially smut-free plants.

The foregoing remarks indicate the difficulty of determining differences in infection caused by environmental or hereditary factors. The division of infection data such as are presented in Tables 3 and 4

into any but very general genetic classes seems unsafe to the writers. Since infection of all susceptible plants is rarely attained in a single test with present technic, a factorial genetic interpretation based on the percentage of infection seems of doubtful validity.

In this study little or no evidence of correlation between morphological characters and resistance to smut infection was observed. This finding corresponds with that obtained in most previous studies of this nature, and indicates that resistance probably is not linked with any character that would interfere with the breeding of resistant varieties having desirable agronomic characters.

SUMMARY AND CONCLUSIONS

The smut-resistant Markton variety of oats was crossed with Early Champion, Ligowa, Scottish Chief, Swedish Select, Iogren, Aurora, and also with Victory, Idamine, and Silvermine. More than 140,000 progeny plants were studied.

In these studies the lemma and the palea were removed from the oat kernel in most cases prior to inoculation with smut. Results have led the writers to the following conclusions:

Markton is extremely resistant to, if not actually immune from, the *Ustilago levis* strain used in these experiments.

The percentages of infection in the nine susceptible varieties varied with the varieties, and the infection percentage of individual varieties was subject to wide fluctuations from year to year.

In seven of nine progeny populations of crosses of Markton (smut free) with smut-susceptible varieties, smut-susceptible and heterozygous plants predominated in F_2, as shown by the breeding behavior of their progenies. In the remaining two, however, in which small populations were grown, the reverse was true.

In three crosses approximately one-fourth of the progeny lines from F_2 plants were smut free and three-fourths infected. In three other crosses almost equal percentages of smut-free and infected progeny lines from F_2 plants were observed.

The results obtained from a study of the several crosses give reason to doubt the existence in Markton of three factors for resistance to all *Ustilago levis* strains.

Such complete gradation of smut percentages occurred within F_3 lines that it seems impracticable to divide these progenies into genetic classes on the basis of percentage of infection.

Correlation between infection percentages in F_3 and F_4 was especially high in the Markton × Scottish Chief cross of which random F_3 material was available for study in F_4. In three other crosses correlation was shown, although random material of the F_3 generation was not available for testing in F_4.

Transgressive segregation for smut infection was observed; that is, the infection percentages in some F_4 lines of the crosses Markton × Scottish Chief and Markton × Swedish Select exceeded the infection percentages of the susceptible parents.

There was little or no correlation between (1) panicle length, (2) kernel length, (3) kernel width, (4) presence of awns, (5) prominence of nerves in lemmas, and (6) lemma color in F_2 plants and the resistance of their progeny to infection by covered smut, *Ustilago levis*.

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THE ANTISCORBUTIC VITAMIN IN HOME-CANNED CARROTS[1]

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INTRODUCTION

Mainly through the experiments of Kohman and Eddy (*3, 4, 5, 7, 8, 9, 10, 11, 12*)[2] we now have considerable data on the vitamin content of commercially canned products. Far less is known of the effect on the vitamins of home canning of fruits and vegetables. Craven and Kramer (*2*) report that in canning Kieffer pears by the cold-pack method there is considerable loss in antiscorbutic potency and that destruction is complete when the open-kettle method is employed. On the contrary, Kramer, Eddy, and Kohman (*12*) found no apparent loss in vitamin C when the same variety of pears was canned commercially after being especially treated to remove oxygen previous to processing. When no special care was taken to remove oxygen beyond the usual practice in commercial canning, there was some loss, 20 and 30 gm. of the canned pear being equivalent to 15 and 20 gm. of the raw product. Experiments by Clow and Marlatt (*1*) indicate that in tomatoes canned by the cold-pack method the loss of vitamin C is slight, whereas in those canned by the open-kettle method the loss is greater. Remy (*13*) found that cauliflower, beans, and carrots which were first cooked in water, then packed in jars with the cooking water and heated in a water bath at 98° C. for one hour, did not protect guinea pigs from scurvy even when fed in doses of 70 gm. daily. Guinea pigs fed peas processed in the same way and tomatoes cold packed and heated at 80° for 20 minutes did not develop the disease.

The purpose of the present study was to determine the difference, if any, of the effect of pressure-cooker and water-bath processing on vitamin C potency. Carrots were used because they are a good source of vitamin C (*6, 14*) and because both methods are employed in the home canning of this vegetable. When the water bath is used it is customary to add a small amount of vinegar or lemon juice to increase the effectiveness of the heating process in killing microorganisms. The carrots tested were canned in three ways, (1) water bath with vinegar, (2) pressure cooker with vinegar, and (3) pressure cooker without vinegar. Although it is not usual to add vinegar when vegetables are processed in the pressure cooker, this variation in method was introduced in order to determine whether a possible difference in the first two lots of carrots was due to a difference in temperature and time of heating or to a difference in hydrogen-ion concentration.

[1] Received for publication May 5, 1931; issued January, 1932.
[2] Reference is made by number (italic) to Literature Cited, p. 1108.

EXPERIMENTAL PROCEDURE

The carrots used in this study were supplied by the department of vegetable gardening of the New York State College of Agriculture. They were grown in sandy soil, harvested at 80 days, and canned a few days after harvesting. Fresh carrots for positive controls were stored in sand in a cold cellar and fed as long as they lasted. Unfortunately, before the completion of the experiment, the store was exhausted, and the fresh carrots fed at the end of the experiment were purchased in the open market.

The carrots to be canned were placed in hot water and boiled for five minutes. They were then dipped in cold water, scraped, and packed in 1-pint glass jars. One teaspoon of salt (5 gm.) was put in each jar, and when acid was to be added, one-half tablespoon (7½ c. c.) of vinegar was used. Finally the jars were filled with boiling water and heated. The processing of the pressure-cooked carrots was carried out under 10 pounds pressure for 40 minutes. The carrots processed in the water bath were heated for 90 minutes.

The pH value of the carrots processed in the pressure cooker without added acid was 4.92, while that of the pressure-cooked carrots to which one-half tablespoon of vinegar had been added was 4.84. The carrots canned with vinegar and heated in the water bath showed a pH value of 4.69. The hydrogen-ion concentration was determined by the electrometric method.[3]

The feeding experiments were conducted with guinea pigs, and the experimental procedure of Sherman, La Mer, and Campbell (*15*) was followed. According to this method normal guinea pigs weighing about 350 gm. are placed in individual cages and fed a basal diet lacking in vitamin C but otherwise adequate. The composition of the basal ration, diet 1, which is approximately that of Sherman and his coworkers, consisted of—

	Per cent
Ground oats	29. 5
Wheat bran	29. 5
Skim-milk powder heated four hours at 110° C	30. 0
Butterfat	10. 0
Sodium chloride	1. 0

To insure a vitamin D sufficiency in some of the later experiments, cod-liver oil replaced 2 per cent of the butterfat. This diet is designated in the tables as diet 2. The animals were weighed twice weekly and the food consumption was recorded. At the end of the experimental period of 91 days the animals that survived were killed. Autopsies were performed on all animals at death and the degree of scurvy determined, this being designated by one, two, and three plus signs according to the degree of abnormality noted, and a minus sign when the autopsy revealed no symptoms of scurvy. This evaluation of the degree of scurvy was based upon the severity of subcutaneous hemorrhages and hemorrhages in the joints, muscles, and viscera, upon the fragility of the long bones, looseness of teeth, and enlargement of the costochondral junctions.

To determine the minimum amount of raw carrot required to prevent scurvy, the ration devoid of vitamin C was supplemented

[3] The writer wishes to thank Prof. T. J. McInerney, of the Department of Dairy Industry, New York State College of Agriculture, for determining the pH values of the carrots.

daily, including Sunday, by various amounts of carrot, namely, 5, 10, 15, 20, 30, 40, 50, and 70 gm. Animals receiving only the basal diet served as negative controls. Two series of animals were fed, respectively, 5 and 10 gm. of the carrots canned by the methods previously described. For each series there was a negative control group that received only the basal diet and a positive control group that received raw carrots. A few animals were fed larger amounts (15, 20, 30, and 50 gm. daily) of the raw and canned carrots. In feeding the canned carrots, the juice was not included. This procedure, which undoubtedly resulted in the loss of some of the water-soluble vitamin C, was adopted because the average housewife serves this vegetable without the juice.

EXPERIMENTAL RESULTS

A summary of the results of the feeding experiments with guinea pigs receiving graded amounts of raw carrot is presented in Table 1.

TABLE 1.—*Results of experiments with guinea pigs receiving basal diet 1 plus graded amounts of raw carrot*

Animal No.	Raw carrot fed daily	Basal diet consumed	Body weight			Period of survival	Degree of scurvy
			Initial	Maximum	Final		
	Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Days*	
M39	None.	337	353	353	211	28	+
F43	None.	275	343	343	230	27	++
M53	None.	657	317	374	208	41	+++
F61	None.	526	295	332	181	35	+++
M165	None.	253	368	368	206	27	+++
M167	None.	386	346	346	192	35	+++
M195	None.	510	329	407	200	37	+++
F50	5	1,292	310	345	311	91	+
F60	5	1,364	323	347	300	91	+
M157	5	1,487	378	435	396	91	−
M168	5	1,317	333	424	366	91	++
M202	5	1,279	360	427	295	91	−
F49	10	1,275	339	404	367	91	−
F56	10	1,540	320	376	366	91	−
M158	10	1,388	348	406	375	91	++
M166	10	1,001	360	360	316	84	+
M200	10	1,010	357	357	213	81	−
F32	15	1,573	286	459	459	91	−
F57	15	1,578	309	419	415	91	−
F156	15	1,307	337	337	332	91	+
M193	15	1,352	353	401	317	91	−
M196	15	1,981	332	651	651	91	−
M31	20	1,804	366	542	542	91	−
F48	20	1,591	325	476	475	91	−
M54	20	1,932	291	611	611	91	−
F155	20	1,356	367	427	427	91	−
M159	20	1,398	342	530	530	91	−
M199	20	1,325	333	502	430	91	−
F44	30	1,790	303	542	542	91	−
F45	30	1,600	318	495	495	91	−
F59	30	1,775	294	597	597	91	−
F160	30	956	341	343	326	91	−
M163	30	1,549	341	543	536	91	−
F194	30	867	381	352	309	91	−
M30	40	939	290	367	340	91	−
M55	40	1,591	299	574	574	91	−
M33	40	1,860	337	600	600	91	−
M52	50	1,861	310	658	658	91	−
F161	50	1,022	354	388	368	91	−
M164	70	1,271	359	593	593	91	−
M203	70	1,628	361	673	673	91	−

Seven negative controls had an average survival period of 33 days. All of the animals developed acute scurvy and five of these had very severe cases. All the animals receiving 5 gm. of raw carrot survived

until the end of the experiment. Of the 5 animals receiving this supplement, 2 showed no scurvy symptoms at autopsy and 2 had only mild cases of the disease. In the group of five guinea pigs receiving 10 gm. of raw carrot one animal died at 81 days and another at 84 days. The other three survived the experimental period. Two animals in this group showed definite symptoms of scurvy, but one of these had a mild case. All the animals receiving 15 gm. of carrot lived throughout the test period and only one developed a mild case of scurvy. None of the animals receiving 20 to 70 gm. of carrot showed any evidence of the disease. It would therefore appear that somewhat more than 15 gm. of raw carrot are required to protect a guinea pig completely against scurvy.

TABLE 2.—*Results of experiments with guinea pigs receiving 5 gm. of raw or canned carrots as the sole source of vitamin C*

Animal No.	Basal diet	Basal diet consumed	Daily supplement to basal diet	Body weight			Period of survival	Degree of scurvy
				Initial	Maximum	Final		
		Grams		*Grams*	*Grams*	*Grams*	*Days*	
M139	1	154	None	300	300	206	19	+
M140	1	180		313	313	185	20	++
F149	1	275		384	384	239	28	++
M152	1	268		301	319	219	26	++
F295	2	341		322	345	191	38	+++
M130	1	324	Raw carrot	319	319	186	34	+
F133	1	283		311	321	199	30	−
M143	1	170		328	328	170	25	−
M146	1	620		336	336	169	56	+
M315	2	674		344	430	275	52	+++
F131	1	134	Canned carrot, water bath, with vinegar	318	318	175	19	+
F135	1	309		300	300	243	27	++
M137	1	350		303	318	188	33	+
M144	1	403		339	362	230	30	++
F150	1	171		314	314	213	20	(a)
M264	2	290		337	337	171	34	++
M134	1	353	Canned carrot, pressure cooker with vinegar	345	352	217	30	++
F141	1	212		304	304	204	24	+
M142	1	182		340	340	216	24	+
M145	1	409		307	327	230	32	(a)
M237	2	439		333	333	184	41	++
M316	2	437		359	422	225	35	+++
F132	1	239	Canned carrot, pressure cooker, without vinegar	329	329	199	27	++
F136	1	208		348	348	208	26	++
F147	1	376		327	337	227	30	+++
M153	1	239		303	303	184	26	−
M278	2	453		344	363	221	41	+++
F313	2	268		355	375	240	33	++

(a) No autopsy.

In Tables 2 and 3 are recorded the results of feeding tests with 5 and 10 gm., respectively, of the carrots canned by the three methods, together with the positive and negative controls. These amounts of raw carrot were smaller than were required for complete protection from scurvy. Ten grams of raw carrot were, however, sufficient to maintain weight throughout the test period and 5 gm. gave growth just below maintenance. Decreased growth is perhaps a better quantitative indicant of the amount of vitamin C present tnan are other symptoms of the disease. Considering that the maintenance level is the most sensitive one at which to measure differences in vitamin C, 5 and 10 gm. of carrot were chosen as the amounts to feed in the comparisons of raw and canned carrots. For each series there is a negative control group receiving only the basal diet free from vitamin

C, and a positive control group receiving raw carrot. None of the animals that received 5 gm. of raw carrot (Table 2) survived the test period. The carrots fed to these animals were purchased in the local market, since the supply of raw carrots from the lot used in canning was exhausted. Whether the difference in the antiscorbutic potency of the two lots of carrots was entirely due to length of time in storage or in part to a difference in the vitamin C content of the original vegetable is not known.

TABLE 3.—*Results of experiments with guinea pigs receiving 10 gm. of raw or canned carrot as the sole source of vitamin C*

Animal No	Basal diet	Basal diet consumed	Daily supplement to basal diet	Body weight			Period of survival	Degree of scurvy
				Initial	Maximum	Final		
		Grams		*Grams*	*Grams*	*Grams*	*Days*	
M175	1	541	None	369	369	228	40	+++
M186	1	686		326	439	258	40	+++
M190	1	365		358	358	211	33	++
M192	1	660		332	389	227	42	+++
M295	2	341		322	345	191	38	+++
F458	1	123		361	361	217	24	+++
M179	1	1, 189	Raw carrot	343	343	318	91	−
M184	1	1, 259		332	332	285	91	+
M189	1	1, 105		374	374	357	91	−
F291	2	1, 013		322	322	310	91	−
M169	1	751	Canned carrot with vinegar (water bath).	367	438	241	43	+++
M170	1	607		332	334	208	52	++
M172	1	747		354	398	245	46	+++
M174	1	861		333	362	226	60	+++
M183	1	482		328	328	197	42	+++
M265	2	235		319	319	194	28	+
F456	1	170		368	368	203	27	+++
M171	1	501	Canned carrot with vinegar (pressure cooker).	342	342	205	45	+++
M181	1	330		323	323	255	32	+++
M182	1	301		376	431	246	42	+++
M185	1	474		333	333	207	38	+++
M191	1	493		358	359	220	37	+++
M280	2	379		331	351	197	35	++
M173	1	394	Canned carrot without vinegar (pressure cooker).	330	330	185	40	+
M176	1	409		376	376	217	35	++
M177	1	470		341	341	209	38	+++
M178	1	522		335	335	200	38	++
M188	1	412		342	342	209	32	+++
M286	2	538		329	378	202	45	+++

The average survival period of the negative control group in Table 2 was 26 days. The survival periods for the groups receiving (1) carrots heated in the water bath, (2) those processed in the pressure cooker and canned with vinegar added, and (3) those processed in the pressure cooker but canned without added vinegar, are 27 days, 31 days, and 31 days, respectively. The canned carrots only slightly prolonged the survival period. It will be recalled (Table 1) that all the animals receiving 5 gm. of raw carrots from the same source as those used in canning, lived throughout the experiment. Upon autopsy all but one of the animals receiving 5 gm. of canned carrots showed definite symptoms of scurvy, and in most cases the condition was severe.

The average survival of the control group in Table 3 was 36 days. This series of tests was conducted at a later period than those summarized in Table 2, in which the average survival of the control group was 26 days. The difference in survival was probably due to the greater vigor of the animals in the series receiving 10 gm. of carrot, assuming that the basal diet used in the series was free from vitamin C.

The different groups within the series are, nevertheless, comparable. The guinea pigs that received carrots canned by the water-bath process lived, on an average, seven days longer than the control group, whereas both groups that received carrots canned by the pressure-cooker method lived only two days longer than the controls. Most of the animals that received 10 gm. of carrots canned by any one of the three methods studied showed severe symptoms of scurvy in the post-mortem examinations, and all showed some symptoms. The average weight increases or decreases of the guinea pigs that received 10 gm. of raw and canned carrot are shown in Figure 1. The gains of the animals that received canned carrots are little better

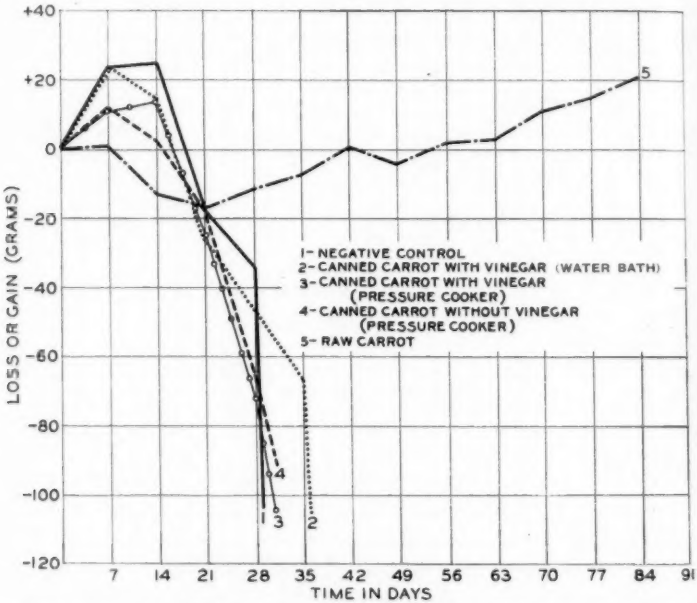

FIGURE 1.—Average weight increases or decreases of guinea pigs receiving 10 gm. of raw and of canned carrot as the sole source of vitamin C. During the first week on the diet there was a marked drop in the weight of the animals due to the elimination of bulky foods from the caecum and adjustment to new surroundings. To eliminate this period of adjustment the zero point is taken one week after the animals were placed on the experimental diet. The last point on the curves is the average survival and weight at death.

than those of the negative control group. The canned carrots apparently retained very little of their original vitamin C potency.

A few data were obtained by feeding larger portions of the various kinds of carrots. These data are summarized in Table 4. Increasing amounts of the carrots canned by the different methods usually resulted in slightly increased growth of the animals and also in longer survival periods, indicating that there is a small amount of vitamin C present in the canned carrots. The data in Tables 2 to 4 and Figure 1 suggest that the carrots processed in the water bath were slightly higher in vitamin C than those processed in the pressure cooker. The animals that received the former lived in general somewhat longer and made better growth than those that received the

latter. The higher temperature of the pressure cooker, though maintained for only 40 minutes, was slightly more destructive to vitamin C than the lower temperature of the water bath, even though the heating was continued more than twice as long. There was no difference measurable by the method employed between the vitamin C potency in carrots processed in the pressure cooker, with and without vinegar. Evidently the increase in hydrogen-ion concentration is not sufficient to reduce the destruction that takes place when the carrots are heated for 40 minutes under 10 pounds pressure.

TABLE 4.—*Results of experiments with guinea pigs receiving basal diet 2 plus 15, 20, 30, and 50 gm. of raw or canned carrot*

Animal No.	Basal diet consumed	Daily supplement to basal diet	Body weight			Period of survival	Degree of scurvy
			Initial	Maximum	Final		
	Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Days*	
RAW CARROT							
F295	341	None.	322	345	191	38	+++
F290	826	15	321	353	245	79	−
M292	1,764	20	382	542	542	91	−
M300	1,192	30	328	452	452	91	−
M296	1,684	50	342	690	690	91	−
CANNED CARROT, WATER BATH, WITH VINEGAR							
M271	323	15	375	375	197	42	++
M272	547	20	369	369	271	49	+++
M307	418	30	323	327	204	56	++
M294	940	50	363	425	287	87	++
CANNED CARROT, PRESSURE COOKER, WITH VINEGAR							
M288	356	15	328	364	222	35	+++
F293	322	20	362	372	295	40	++
M299	608	30	320	357	233	57	++
M301	500	50	340	319	207	56	+++
CANNED CARROT, PRESSURE COOKER, WITHOUT VINEGAR							
M287	491	15	348	403	286	38	++
M308	496	20	348	387	255	44	+++
F306	452	30	334	414	300	47	+++
M297	507	50	335	412	260	53	+++

SUMMARY

In this study the vitamin C content of home-canned carrots was compared with that of the raw vegetable. The preventive method of Sherman, La Mer, and Campbell was employed. Three methods used in the canning of carrots were studied. The results indicate that practically all the vitamin C present in raw carrots is destroyed when carrots are cold packed with a small amount of vinegar and heated in a water bath for 90 minutes, or are processed with or without vinegar in a steam-pressure cooker for 40 minutes at 10 pounds pressure. A daily dose of 15 to 20 gm. of raw carrot was required to protect a guinea pig from scurvy, but even when 50 gm. of canned

carrot were fed most of the animals developed severe cases of scurvy, as indicated by post-mortem examination, and all of them died before the end of the test period. There was no difference noted in the carrots processed in the pressure cooker with and without the addition of acid.

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THE ANTISCORBUTIC VITAMIN IN THE JUICE OF HOME-CANNED TOMATOES [1]

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INTRODUCTION

In an earlier study on carrots published in this journal (*10*), [2] it was shown that home canning, by either the water-bath or the pressure-cooker method, destroys practically all of the antiscorbutic vitamin present in the raw carrots. Carrots are representative of the so-called nonacid [3] class of foods, the pH value of those used in the study ranging from 4.69 to 4.92. The increased rate of destruction, especially in vitamin C, by heat and oxidation in the presence of added alkali has been amply demonstrated by the work of Harden and Zilva (*6*), Delf (*3*), Hess and Unger (*7*), La Mer, Campbell, and Sherman (*8*), and others. It was considered of interest, therefore, to determine the effect of home canning on a food having a natural hydrogen-ion concentration greater than that of carrots. Tomatoes were chosen for the investigation as a typical acid fruit. Only the water-bath method was studied, as the pressure cooker is rarely, if ever, employed in the home canning of tomatoes. Four jars of tomatoes chosen at random from the tomatoes used in the feeding tests had pH values, respectively, of 4.09, 4.12, 4.16, and 4.16.[4]

Craven and Kramer (*2*), working with Kieffer pears which had a pH value of 4, and therefore a somewhat greater acidity than tomatoes, concluded that the antiscorbutic potency of pears is destroyed by open-kettle canning. By the cold-pack method destruction is not complete; but of pears canned by this method, even 22.5 gm. fed daily did not protect guinea pigs from scurvy, while 10 to 15 gm. of the raw pear was sufficient. Clow and Marlatt (*1*) found a slight loss of vitamin C in tomatoes canned by the cold-pack method, but when the open-kettle method was employed the loss in vitamin C was much greater. In some experiments on the destruction of the antiscorbutic vitamin by heat, Givens and McCluggage (*5*) showed that while only 2.5 gm. of raw tomatoes sufficed to prevent scurvy in guinea pigs, 10 gm. of canned tomatoes, processed for one-half hour at 250° F., was required. This temperature is considerably higher and the time of heating is longer than are necessary for the successful preservation of tomatoes. Delf (*4*) canned tomatoes by first heating the fruit in a shallow pan for 10 minutes and then packing it in jars and processing it in a bath at 100° C. for 5 minutes. Of the tomatoes canned in this manner, 8.5 c.c. was required to protect guinea pigs from scurvy, whereas of the fresh tomatoes 2 c.c. was sufficient.

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[1] Received for publication May 5, 1931; issued January, 1932.

[2] Reference is made by number (italic) to Literature Cited, p. 1113.

[3] Carrots are usually classified as a "nonacid" food. With a pH close to 5, they are actually acid in reaction. According to Wherry (*11*), both carrots and tomatoes fall in the "mediacid" range (pH 4 to 5).

[4] The writer is indebted to Dr. P. F. Sharp, of the Department of Dairy Industry, New York State College of Agriculture, in whose laboratory the pH values of the tomatoes were determined.

EXPERIMENTAL PROCEDURE

Two varieties of tomatoes were used in this investigation, Globe and Bonny Best.[5] They were grown outdoors and were vine ripened. Since fresh tomatoes from the garden were not available throughout the experiment, some of the raw tomatoes used in the feeding tests were purchased in the local market. The tomatoes were canned within a day after picking. They were first immersed in hot water for 2 minutes, then peeled, and while still warm packed whole in ½-pint glass jars and pressed down firmly so that the jars were well filled. One-half teaspoon of sodium chloride (2.5 gm.) was added to each jar. The jars were partly sealed and placed in a water bath at 80° C. The water bath was then brought to the boiling point as rapidly as possible, usually in about 4 minutes, and the boiling continued for 20 minutes. At the end of that time the jars were removed from the bath and allowed to cool, in the air, to room temperature. This usually required about 1 to 1½ hours. The highest temperature at the center of the jar was 95°, which was reached after 15 minutes of boiling. The experiment was completed within six months after the tomatoes were canned, so that none of the tomatoes were stored longer than six months and most of them for a shorter period. Only the juice of the tomatoes was used in the feeding tests. This was prepared by first putting the fruits through a meat chopper, then pouring through cheesecloth, and finally through coarse filter paper.

The feeding experiments were conducted in the usual way, following the procedure of Sherman, La Mer, and Campbell (*9*). Guinea pigs, weighing 300 to 400 gm. each, the average weight for each group approximating 350 gm., were fed a basal diet consisting of skim-milk powder (heated at 110° C. for four hours), 30 per cent; ground whole oats, 29. 5 per cent; wheat bran, 29.5 per cent; butterfat, 10 per cent; and sodium chloride, 1 per cent. A negative control group was given only the basal diet and distilled water. The remaining animals received in addition 1 to 4 c. c. of either raw or canned tomato juice. This was fed daily, including Sunday, by means of a pipette. At the end of the experimental period of 91 days the animals that survived were killed. Autopsies of all animals were made to determine the severity of scurvy symptoms. The postmortem examinations were conducted as outlined by Sherman, La Mer, and Campbell (*9*), observations being made of the typical signs of scurvy, notably hemorrhages of the muscles, enlargement of the joints, fragility of the bones, and looseness of the teeth. The degree of scurvy is designated in the tables by one, two, or three plus signs, depending upon the severity of the symptoms. A negative sign indicates the absence of scurvy.

RESULTS

In Table 1 is shown the quantity of food consumed by each guinea pig, the initial, maximum, and final weights of each animal, the period of survival, and the degree of scurvy.

It is apparent from the data in the table that 3 c. c. of raw tomato juice was almost sufficient to protect a guinea pig from scurvy. All the animals that received this quantity lived until the end of the experimental period, and only one developed a mild case. Four c. c.

[5] The tomatoes used in this study were furnished by the Department of Vegetable Gardening of the New York State College of Agriculture.

completely protected all the animals. It may therefore be said that the minimum protective dose of the raw tomato juice used in this study was approximately 3.5 c. c. The table also shows that 4 c. c. of canned tomato juice did not prevent scurvy. Of the three animals

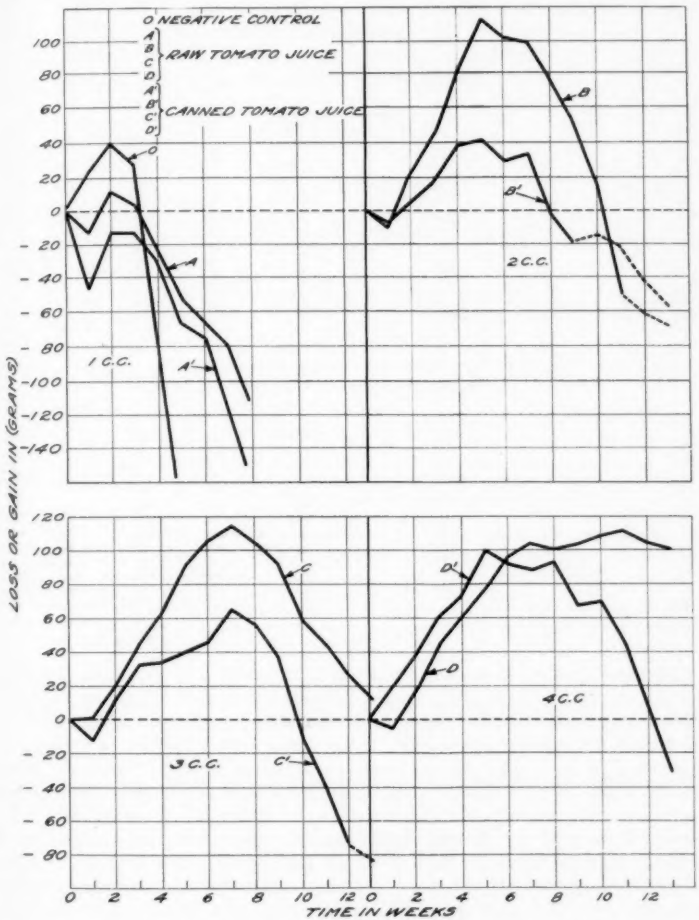

FIGURE 1.—Average weight increases or decreases of guinea pigs receiving different quantities of raw and canned tomato juice. The change in weight for the groups is represented by a solid line, terminating with the first death. A broken line represents the average weights of the surviving animals. In the negative control group and the groups receiving 1 c. c. of raw or canned tomato juice all animals died before the end of the experiment. The last point on each of these curves is the average survival and weight at death

that received this quantity, two survived to the end of the experiment, but upon autopsy both showed definite symptoms of scurvy and one of them had a rather severe case. The third animal died after 86 days on the diet, apparently from scurvy, though no gross pathological symptoms were found.

TABLE 1.—*Results of experiments with guinea pigs receiving different quantities of tomato juice as the sole source of vitamin C*

RAW TOMATO JUICE

Animal No.	Basal diet consumed	Tomato juice fed daily	Body weights			Period of survival	Degree of scurvy
			Initial	Maximum	Final		
	Grams	*C. c.*	*Grams*	*Grams*	*Grams*	*Days*	
M471	401	None.	364	434	200	35	+++
M480	420		335	387	195	33	+++
F491	298		343	369	175	29	++
F496	370		338	349	180	35	++
F464	497	1	332	382	241	39	++
F466	561		365	365	187	56	+
M469	689		351	402	209	50	+
M474	1,434		357	421	325	87	++
M494	467		329	329	212	44	++
F461	1,190	2	331	431	228	78	+
F467	1,658		396	565	281	87	++
M479	1,534		330	444	284	91	−
M495	1,308		344	466	238	77	+
F478	1,420	3	329	425	376	91	+
M492	1,535		364	537	304	91	−
M509	1,412		335	427	386	91	−
M465	1,979	4	341	609	609	91	−
M488	1,638		362	481	422	91	−
F508	1,427		349	424	328	91	−

CANNED TOMATO JUICE

M470	557	1	354	354	193	44	++
F473	579		342	342	194	49	++
M486	949		349	349	217	67	++
F468	1,291	2	361	449	336	91	+
M484	1,005		339	427	327	72	++
M487	1,000		334	395	231	63	+
F489	1,352		336	370	237	91	+
F477	1,209	3	355	405	324	91	−
M483	1,264		338	424	222	89	+
F497	1,445		334	491	240	86	+++
M498	1,167		352	372	216	78	+
F462	1,555	4	364	485	357	91	+
F490	1,077		305	398	211	86	−
M493	1,629		349	477	356	91	+++

Comparisons of the average weight increases of animals receiving equal amounts of raw and canned tomato juice are shown in Figure 1. With every variation in amount of tomato juice, the animals receiving the raw juice grew more rapidly than those receiving the same amount of canned juice. These results are in agreement with those of Craven and Kramer (*2*) on Kieffer pears which had a hydrogen-ion concentration somewhat greater than that of tomatoes. Clow and Marlatt (*1*), on the contrary, found slight loss in vitamin C in the canning of vine-ripened tomatoes when the cold-pack method was used. These authors fed the whole tomato, however, while in the experiments here reported only the juice was fed. By feeding the juice rather than the whole tomato, more uniform sampling is perhaps possible, and the results may be compared with the earlier experiments on tomatoes of Delf and others. It is possible that some destruction of vitamin C occurred in filtering the tomato juice, due to oxidation during the filtering process. However, if there was a loss of vitamin due to the filtration, the results are still comparable, since both the raw and canned products were treated similarly.

SUMMARY

The antiscorbutic potency of the juice of raw and of home-canned tomatoes was compared. The tomatoes were cold packed and processed for 20 minutes. The data presented indicate a considerable loss of vitamin C in the canned product. Three and one-half c. c. of the raw tomato juice was sufficient to protect the guinea pigs from scurvy, while 4 c. c. of the juice of the canned tomatoes failed to protect the animals from the onset of the disease.

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